APLODONTID, SCIURID, CASTORID, ZAPODID AND GEOMYOID RODENTS OF THE RODENT HILL LOCALITY, CYPRESS HILLS FORMATION, SOUTHWEST SASKATCHEWAN

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ABSTRACT

The Rodent Hill Locality is a fossil-bearing site that is part of the Cypress Hills Formation, and is located roughly 15 km northwest of the town of Eastend, Saskatchewan. A number of fossil mammal and other vertebrate taxa are present at Rodent Hill; the primary objective of this project was to identify the fossil rodents of the families Sciuridae, Aplodontidae, Castoridae, Heliscomyidae, Heteromyidae, Florentiamyidae and Zapodidae. These taxa were correlated with rodents from other North American faunas to establish the age of the Rodent Hill Locality.

The species *Haplomys* cf. *H. liolophus, Dakotallomys* cf. *D. pelycomyoides*, *Kirkomys milleri, Proheteromys nebraskensis, Agnotocastor* cf. *A. praetereadens,* and possibly *Cedromus* cf. *C. wilsoni* support the Whitneyan age designation of the Rodent Hill Locality. Taxa that are described from Rodent Hill that are better known from earlier-age sites include *Heliscomys vetus* and *H. hatcheri*, *Ecclesimus* sp. and *Oligotheriomys* sp. Taxa that are younger than Whitneyan but have been recovered at Rodent Hill include *Parallomys* sp., *Plesiosminthus* sp., *Protospermophilus* sp., and *Nototamias* sp. Two new species in the genus *Sciurion,* and one new species in the genus *Pseudallomys* are described, and a new species of *Heliscomys* is identified but not formally named.

The rodents from the Rodent Hill Locality support the Whitneyan age assignment of the site. This is based on the presence of Whitneyan taxa, and the *in situ* co-occurrence of older and younger taxa within the site.

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LIST OF ABBREVIATIONS

Measurements and Statistics:

A-P – Anterior-posterior maximum length.

TR – Maximum transverse width in upper teeth

TRA– Transverse anterior measurement. Indicates the maximum width of the trigonid (anterior portion) in lower teeth.

TRP – Transverse posterior measurement. Indicates maximum width of the talonid (posterior portion) in lower teeth.

LEH – Lingual Enamel Height. In castorid teeth, the height of the lingual enamel.

BEH – Buccal Enamel Height. In castorid teeth, the height of the buccal enamel.

MEAN – The average of a number of measurements.

OR – Operational Range. The range (minimum and maximum) of a series of measurements.

SD – Standard Deviation.

CV – Coefficient of Variation

Institutions:

SMNH – Royal Saskatchewan Museum.

UNSM – University of Nebraska State Museum.

AMNH – American Museum of Natural History.

F:AM – Frick Collection: American Museum of Natural History.

UCMP – University of California Museum of Paleontology.

USNM –National Museum of Natural History, Smithsonian.

SDSM – South Dakota School of Mines and Technology

MCZ – Museum of Comparative Zoology, Harvard University

CM – Carnegie Museum

YPM – Yale Peabody Museum

1. INTRODUCTION

1.1 OVERVIEW

The Rodent Hill Locality is a fossil-bearing site located roughly 15 km northwest of the town of Eastend, Saskatchewan, and is within the Cypress Hills Formation in southwest Saskatchewan. The Cypress Hills Formation contains fossil terrestrial vertebrates representing ages from the middle Eocene to the early Miocene. The vertebrates represented include mammals, birds, reptiles, amphibians, and osteichthyans. These fossils have been collected and described since the late 1800s. The formation is primarily fluvial deposits, the high-energy nature of which has resulted in the majority of the fossil remains being disarticulated bones and isolated dental elements. Dental elements are the most reliable fossils for identifying the small mammals, which as a group are the most appropriate source for biostratigraphic correlation with other Tertiary terrestrial faunas in North America.

The objectives of this project are to identify the rodents of the families Sciuridae, Aplodontidae, Castoridae, Heliscomyidae, Heteromyidae, Florentiamyidae and Zapodidae from the Rodent Hill Locality of the Cypress Hills Formation, and correlate these taxa elsewhere in North American faunas to establish the age of the Rodent Hill Locality.

1.2 RESEARCH IN THE CYPRESS HILLS

1.2.1 Geology Of The Cypress Hills

The Cypress Hills Formation of southwest Saskatchewan and southeast Alberta is a Tertiary terrestrial fluvial deposit (Leckie and Cheel, 1989) that is approximately 1100 km^2 in area. The modern hills are an erosional remnant that was not eroded in the late Tertiary (Dawson, 1875a) and consist of sands and gravels, up to boulder-size sediments in some areas, alternating with muds and sandy muds as well as debris flow sediments (Leckie and Cheel, 1989; Storer, 1996). Some of these sediments are lithified into sandstones and conglomerates (Leckie and Cheel, 1989) while the sediments of other areas are unconsolidated. These sediments may have been deposited over a period of 28 Ma based on the fossil mammal record (Storer and Bryant, 1993), resulting in a deposit that now averages 38 m thick, and may be up to 76 m thick (Vonhoff, 1965a, b). Nurkowski (1984) estimated that as much as 180 m of sediment eroded away by the east-flowing streams during the deposition of the Cypress Hills Formation. The Cypress Hills Formation overlies older Cretaceous or Paleocene strata (Kupsch, 1956), separated by a disconformity. In some areas the Cypress Hills Formation overlies the Paleocene Ravenscrag Formation, but in other areas the Paleocene strata have been eroded, and the Cypress Hills Formation overlies the Cretaceous Bearpaw or Frenchman Formations (Kupsch, 1956).

These deposits are non-marine in origin based upon the sedimentary facies and the fossil vertebrates that have been recovered, including freshwater fishes, land turtles, amphibians, lizards, mammals and birds. The sedimentology of the Cypress Hills Formation is also supportive of a fluvial, non-marine depositional environment (Leckie and Cheel, 1989).

Interpretations of the deposition of the Cypress Hills Formation have included valley-confined stream deposits (Howard, 1960); deposits of a meandering channel (Vonhoff, 1965a, b; 1969); and deposits from powerful streams into temporary lakes and backwaters (Russell, 1972). The most recent interpretation of the Cypress Hills Formation is a braidplain deposit with sediment transported from the southwest, in particular the Rocky Mountains of northwestern Montana, with some input from the Bearpaw and Highwood Mountains of central and northern Montana (Leckie and Cheel, 1989). Evidence for the braidplain interpretation comes from the long distance between sand and gravel deposits, and the low variability of maximum grain sizes (Leckie and Cheel, 1989).

The braided streams that transported the sediments to be deposited in the Cypress Hills headed in the Highwood and Bearpaw Mountains and the Sweetgrass Hills (Leckie and Cheel, 1989). Several valleys channeled the braided streams that occasionally shifted laterally, reworking older strata and depositing the gravel sheet that typifies the Cypress Hills Formation. The majority of the deposits from these events have been eroded, preserving only a small area as the Cypress Hills and Swift Current plateaus (Leckie and Cheel, 1989).

Recent work by Frank McDougall (pers. comm.), University of Saskatchewan, using surface exposures and drill cores near Eastend have indicated a topography at the beginning of deposition of the Cypress Hills Formation that is similar to that of the present day. With the increase in deposition over time, the valleys were infilled, transforming the steep, hilly terrain into a flatter braidplain.

1.2.2 History of Research in the Cypress Hills

Dawson (1875a, b; 1881) gave the first accounts of the Cypress Hills during a geological survey of the area, but the first detailed descriptions of the area were by McConnell (1885) who first surveyed the area in 1883 and subsequently described the first Tertiary fossils from the region. The geology of the Cypress Hills was later studied by Weston (1895), Davis (1918), McLearn (1928), Williams and Dyer (1930), Russell (1940b, 1950a, 1950b, 1951, 1953, 1957), Wood (1949), Furnival (1950), Kupsch (1956), Howard (1960), Vonhoff (1965, 1969), Eisenbacher (1977); Storer (1978b), Vreeken *et al.* (1989) and, Leckie and Cheel (1989, 1990).

The vertebrate fossils in the Cypress Hills of Saskatchewan have been extensively studied since first being described by McConnell (1885). The earliest detailed works about Tertiary fossils were by Cope (1885, 1886, 1889a, 1889b, 1891), Ami (1891) and Lambe (1905a, 1905b, 1905c, 1908). Later studies of the vertebrate fossils from the Cypress Hills Formation were reported by Matthew (1903), Sternberg (1924), Russell and Wickenden (1933), Russell (1934, 1936, 1938, 1940a, 1965, 1972, 1975, 1976, 1978, 1980a, 1980b, 1982, 1984), Wood (1949, 1961), Weigel (1963), Holman (1963, 1968, 1972, 1976), Lundberg (1975), Storer (1970, 1975a, 1975b, 1978a, 1981a, 1981b, 1984a, 1984b, 1987, 1988, 1990, 1992, 1993, 1995, 1996, 2002), Emry and Storer (1981), Krishtalka *et al.* (1982), Skwara (1986, 1988), Bryant (1991, 1992, 1993), Storer and Bryant (1993, 1997), Eberle and Storer (1995); Rothecker and Storer (1996), Williams and Storer (1998), Meyer (2003, *unpub.*) and Rothecker (2003, *unpub.*). The rodents from the Cypress Hills were mentioned in many of these studies (e.g. Russell, 1972; Skwara, 1986; Storer, 1978a, 2002; Williams and Storer, 1998; Meyer, 2003; Rothecker, 2003), but only Meyer (2003) and Rothecker (2003) were specific to Orellan or Whitneyan faunas, respectively.

The presumed age of the Cypress Hills fossil sites has varied throughout the history of their study. McConnell (1885) assigned the Cypress Hills a Miocene age (the North American Land Mammal Ages did not yet exist). Other researchers interpreted the fauna as Oligocene or lower Miocene (Cope, 1891), early Oligocene (Matthew, 1903) and Oligocene (Lambe, 1908). Lambe (1905b) suggested that the diversity of equid taxa he described could refer to a wider range of ages than those previously considered, which would have corresponded to the “ages” Chadronian, Orellan and Whitneyan, but subsequent collectors continued to recover fossils without acquiring the necessary stratigraphic detail. The predominant assumption was that the Cypress Hills Formation represented only the Chadronian, as this is the most common age of fossils recovered in the formation (Storer and Bryant, 1993). In 1941, the Wood Committee (Wood *et al.*, 1941) identified the Cypress Hills Formation as a paratype of the Chadronian Land Mammal Age (Wood *et al.,* 1941), at that time considered earliest Oligocene. Based on the presence of brontotheres, Russell (1965) noted the faunal similarities with sites in South Dakota and maintained that the Cypress Hills Formation represented a similar Chadronian age.

A few Cypress Hills Formation sites were assigned ages that were not Chadronian; these included the Swift Current Plateau that was studied by Russell and Wickenden (1933) and later assigned a Uintan age by Storer (1978b); and the Hemingfordian-age Topham Local Fauna (Skwara, 1986, 1988). The majority of the Cypress Hills Formation continued to be considered Chadronian, as exemplified by a stratigraphic column in Leckie and Cheel (1989) (**Figure 1.1**). In this figure they describe the deposition of the Cypress Hills Formation as occurring over two events, one extending from the Uintan through to the Duchesnean and the Chadronian, and one in the Hemingfordian. In between these depositions is depicted an extensive gap in the

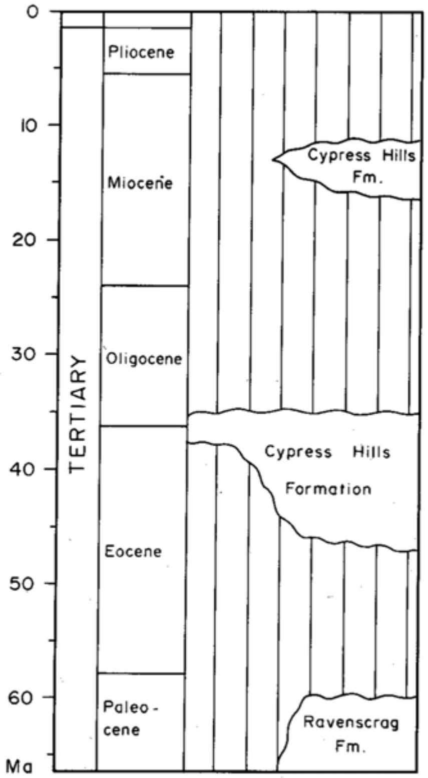


Figure 1.1 Stratigraphic column from Leckie and Cheel (1989), showing the very large Oligocene unconformity that was thought to be present in the Cypress Hills.

sequence where information about the Orellan, Whitneyan, and Arikareean was apparently missing.

The conclusion that the majority of the Cypress Hills Formation represented a single age—Chadronian—was based on assumptions that all fossils came from the same stratigraphic horizon, that biostratigraphic zonation was not possible in the southwest Saskatchewan Cypress Hills, and that all of the Cypress Hills material represented deposits of the same age (Storer and Bryant, 1993). Although there was the potential for these assumptions to be correct, later work would prove them false.

In 1963, B. A. McCorquodale, at the Saskatchewan Museum of Natural History (now the Royal Saskatchewan Museum) measured a series of sections throughout the Cypress Hills Formation and collected fossils with stratigraphic control, but these were not made available until thirty years later starting with work on the fossil horses from the area (Storer and Bryant, 1993). Once this work was studied at the RSM, the span of time represented in the Cypress Hills Formation was recognized as being more complete than previously thought.

The importance of the Cypress Hills Formation faunas has increased due to the recognition of Tertiary mammal fossils that extend from the middle Eocene to the middle Miocene (Uintan to Hemingfordian) in a relatively continuous stratigraphic sequence (Storer and Bryant, 1993) with smaller disconformities representing shorter spans of missing time. Among the most notable are sites that are Orellan and Whitneyan (early Oligocene), ages that are not extensively represented throughout North America (Emry *et al.*, 1987). The Rodent Hill Locality has been regarded as Whitneyan in age (Storer and Bryant, 1993; Storer, 1996), a designation that will be tested here based on the rodent taxa identified.

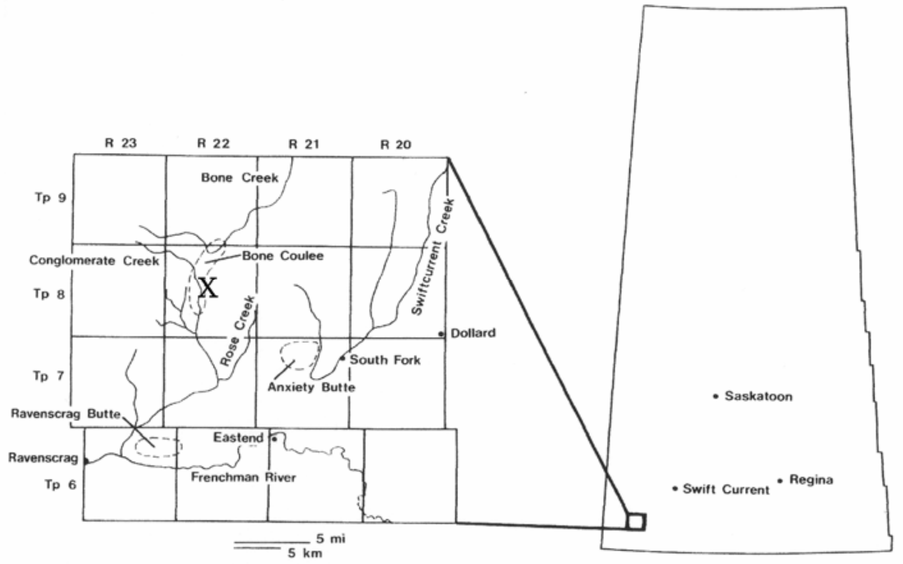
More recently, Rothecker (2003) studied two families of rodents, the Cricetidae and Eomyidae, and found that the taxa from these families offered strong support that the Rodent Hill Locality represents a Whitneyan-age fauna.

1.3 THE RODENT HILL LOCALITY

1.3.1 Location of the Rodent Hill Locality

The Rodent Hill Locality is a site located in Bone Coulee, 10 km northwest of the town of Eastend, southwest Saskatchewan **(Figure 1.2)**. It is one of several sites in Conglomerate Creek, which consists of sites ranging in age from middle Chadronian to Hemingfordian (Storer, 1996). Rodent Hill is a road cut in a section known as the “titanothere section”. The lowest site in the section is a Chadronian age quarry from which a titanothere skeleton was collected. Stratigraphically superior to this site, the Orellan-age Fossil Bush Locality is present, followed vertically by the Rodent Hill Locality. Capping the section, there is a Hemingfordian-age site (Storer, 1996; Storer and Bryant, 1993).

Figure 1.2 Map of the Rodent Hill Locality, marked with an X. Adapted from Storer and Bryant (1993), modified by Rothecker (2003).



1.3.2 Fossils at the Rodent Hill Locality

There have been several collections of fossils from the site. McCorquodale first collected and described the "Titanothere" section while measuring localities in the Cypress Hills in 1963 (Storer and Bryant, 1993) but the material was not published or made available until much later. Russell (1972) refers to material from the Rodent Hill Locality, but Storer found that those fossils were probably mixed with specimens collected from the nearby Fossil Bush Locality and an unknown Chadronian-age site. Various workers made subsequent collections for the Royal Saskatchewan Museum in the 1990s, and more recently collections for this study were made there in 2000 and 2001.

Most fossils were obtained from the site by surface collecting matrix that was then power screened and later picked through in a lab. Although the majority of the material was collected without consideration of stratigraphic location on the site, some collections differentiated between fossils collected above and below the weathering-resistant bench that is a prominent feature of the site. Only the material collected in 2001 was controlled stratigraphically to determine any faunal changes within the site.

Table 1.1 Preliminary list of fossil mammal taxa identified from Rodent Hill. From Storer, 1996.

- Order Didelphimorpha
  - Family Didelphidae
    - *Herpetotherium* sp.
- Order Leptictida
  - Family Leptictidae
    - *Leptictus* sp.
- Order Insectivora
  - Family Proscalopidae
    - Proscalopidae, gen. et sp. indet.
  - Family Soricidae
    - Soricidae, gen. et sp. indet.
- Order Carnivora
  - Family Nimravidae
    - *Dinictis* sp.
  - Family Mustelidae
    - Mustelidae, gen. et sp. indet.
  - Family Amphicyonidae
    - *Daphoenus* sp.
  - Family Canidae
  - ?*Hesperocyon* sp.
- Order Perissodactyla
  - Family Equidae
    - *Miohippus* nr. *M. equiceps* (Cope, 1879)
  - Family Rhinocerotidae
    - *Diceratherium* sp.
- Order Artiodactyla
  - Family Leptochoeridae
    - *Leptochoerus* sp.
  - Family Anthracotheridae
    - *Elomeryx* sp.
  - Family Agriochoeridae
    - *Agriochoerus* sp.
  - Family Merycoidodontidae
    - Merycoidodontidae, gen. et sp. indet.
  - Family Protoceratidae
    - *Protoceras* sp.
  - Family Leptomerycidae
    - *Leptomeryx* sp.
    - *Pronodens* sp.
- Order Rodentia
  - Family Aplodontidae
    - *Prosciurus relictus* (Cope, 1877)
    - Aplodontidae, gen. et sp. indet.
  - Family Cricetidae
    - *Eumys brachyodus* (Wood, 1937)
  - Family Eomyidae
    - *Namatomys* sp.
    - *Paradjidaumo* sp.
  - Family Heteromyidae
    - *Proheteromys* sp.
- Order Lagomorpha
  - Family Leporidae
    - *Palaeolagus* cf. *P. burkei* (Wood, 1940)
    - *Megalagus primitivus* (Dawson, 1958)

Table 1.2. Eomyidae and Cricetidae identified from Rodent Hill. From Rothecker, 2003.

Order Rodentia
  Family Eomyidae
    Leptodontomys bernadettae Rothecker, 2003
    Leptodontomys sp.
    Metadjidaumo harveyi Rothecker, 2003
    Paradjidaumo hypsodus Setoguchi, 1978
    Pseudotheriomys sp.
    Eomyidae gen. et sp. indet, Type A
    Eomyidae gen. et sp. indet, Type B
  Family Cricetidae
    Eumys brachyodus (Wood, 1937)
    Eumys elegans Leidy, 1856
    Wilsoneumys sp.
    Leidymys korthi Williams and Storer, 2003
    Scottimus cf. *S. ambigus* Korth, 1981
    Scottimus sp.

The Rodent Hill Locality is only referred to in a few published studies (Storer, 1995, 1996; Storer and Bryant, 1993, 1997) and none of the fauna is described in detail. Storer (1996) provided a preliminary faunal list from the locality, but the majority of these identifications were not beyond the familial level. The taxa previously identified from Rodent Hill by Storer (1996) are listed in **Table 1.1**.

When Storer (1996) assigned the site an age of Whitneyan, it was primarily based upon a single lagomorph taxon, *Paleolagus* cf. *P. burkei*, a taxon described from the Whitneyan-age Vista Member in Colorado (Dawson, 1958) that is distinguishable by an anteroexternal fold on the p3. Other identified taxa that are also supportive of a Whitneyan age include *Miohippus* near *M. equiceps*, *Eumys brachyodus* and *Megalagus primitivus* (Storer and Bryant, 1997).

Rothecker (2003) studied the rodent families Eomyidae and Cricetidae of Rodent Hill and found several more taxa in these families than first identified by Storer (1996). The identified eomyids and cricetids are listed in **Table 1.2**.

The findings of Rothecker (2003) supported the assignment of Rodent Hill as a Whitneyan site due to the presence of *Eumys brachyodus* and the transitional faunal composition of the site, with taxa that are better known from older (Orellan) or younger (Arikareean) age sites.

1.4 THE NORTH AMERICAN LAND MAMMAL AGES

The fossil localities in the Cypress Hills are biostratigraphically distinguished based on the North American Land Mammal Ages (NALMA) proposed by the Wood Committee (Wood *et al*., 1941). The purpose of this committee was to develop a biostratigraphic framework to divide the entire terrestrial Tertiary of North America into provincial ages based on mammalian faunas. In principle, these ages were supposed to be independent of local lithologies or other stratigraphic schemes (including the epochs or European divisions) and include all of Tertiary time (Wood *et al*., 1941). Some compromises were necessary at the time, including the presence of temporal gaps within the scheme due to a lack of information, the definition of the NALMA ages using local geological formations (14 out of the original 18), and the correlation of the NALMA ages to the Tertiary epochs (Emry *et al.,* 1987). These issues were not enough to outweigh the utility of the system that has allowed for its widespread use among North American paleontologists. Later work has attempted to resolve some of the confusion about the NALMA ages from the original proposal through more detailed stratigraphy and better correlation through absolute dating and magnetostratigraphy, notably in the Eocene and Oligocene (Emry *et al*., 1987; Korth, 1989a, Swisher and Prothero, 1990; Tedford *et al*., 1996; Prothero and Whittlesey, 1998).

A major advancement in the understanding of the correlation of the Eocene and Oligocene NALMA ages is their position relative to the Tertiary epochs. When first proposed by the Wood Committee (Wood *et al*., 1941), the late Eocene was comprised of the Uintan and Duchesnean, while the NALMA ages of the Oligocene were the

Chadronian (oldest), Orellan, and Whitneyan (youngest). Berggren *et al*. (1978) proposed that the Eocene-Oligocene boundary was around 37.5 Ma, based upon ^{40}K/^{40}Ar dating and correlation of European and North American mammal faunas. This date would have allowed for the Chadronian to remain as the basal NALMA in the Oligocene. However, later work pushed the age of the Eocene-Oligocene to much younger dates. Berggren *et al.* (1985) produced a date of 36.6 Ma correlating magnetostratigraphic data with planktonic biostratigraphic data, and ^{40}Ar/^{39}Ar data produced an Eocene-Oligocene boundary age of 34.4 Ma (Swisher and Prothero, 1990; Berggren *et al.*, 1992; Prothero and Swisher, 1992). This date did contrast with Wang (1992) who proposed that the Eocene-Oligocene boundary remain at 36 or 37 Ma based upon early Oligocene Asian mammals that are similar to those from the Chadronian of North America, but Prothero and Swisher (1992) countered that the Chadronian fauna had likely emigrated to Eurasia after first evolving in North America.

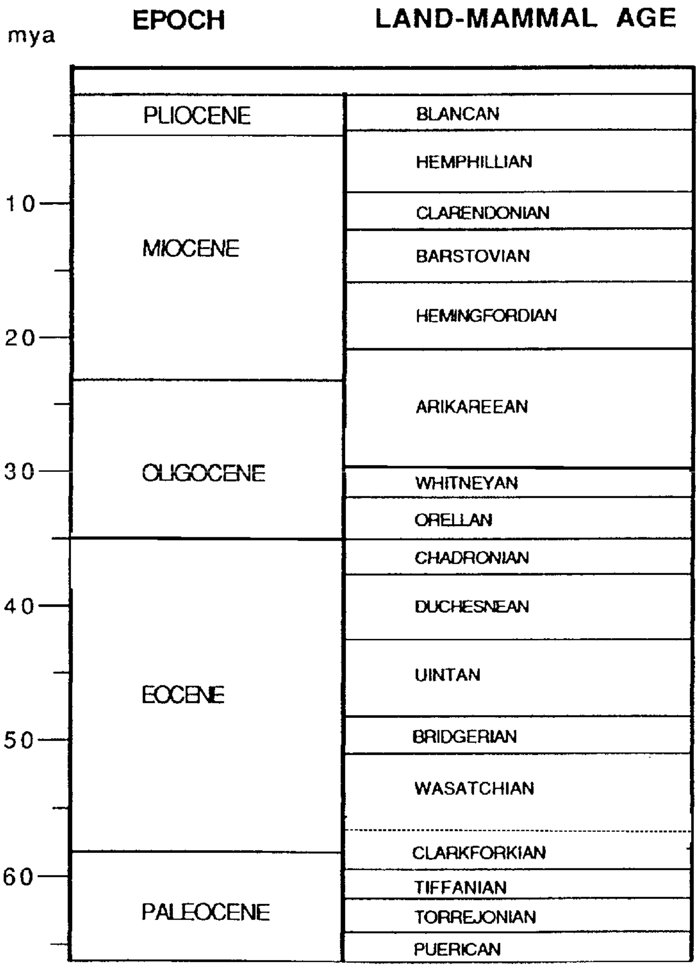


Figure 1.3. The North American Land Mammal Ages of the Tertiary, and the relative positions of the NALMA with the Epochs of the Tertiary. Modified from Korth (1994a).

Swisher and Prothero (1990) also used ^{40}Ar/^{39}Ar to better reconcile the boundaries of the Paleogene NALMA ages (**Figure 1.3**). This work found the boundary dates to be about 34 Ma for the Chadronian-Orellan boundary and about 32 Ma for the Orellan-Whitneyan boundary (Swisher and Prothero, 1990). With these new boundary dates, the Chadronian would be recognized as the last NALMA age in the Eocene, with the Orellan and Whitneyan comprising the earlier part of the Oligocene, and the late Oligocene coinciding with the early Arikareean (Prothero and Swisher, 1992; Prothero, 1996; Prothero and Emry, 1996). These boundaries also allowed for better correlation of

North American mammalian extinction events with the terminal Eocene event in the European marine record (Swisher and Prothero, 1990).

The mammal fauna of North America from the early Chadronian to the early Arikareean are usually included in the White River Chronofauna, although the ancestral elements had become clear as early as the Uintan (Emry *et al.*, 1987). A chronofauna is a natural faunal assemblage in a limited geographic range that is relatively stable for a discernable period of geologic time (Olson, 1952); there may be minor changes in the fauna or flora, but this is usually replacement of early taxa by related forms (Emry *et al.,* 1987). The characteristics of the faunas from the Chadronian through the Orellan and

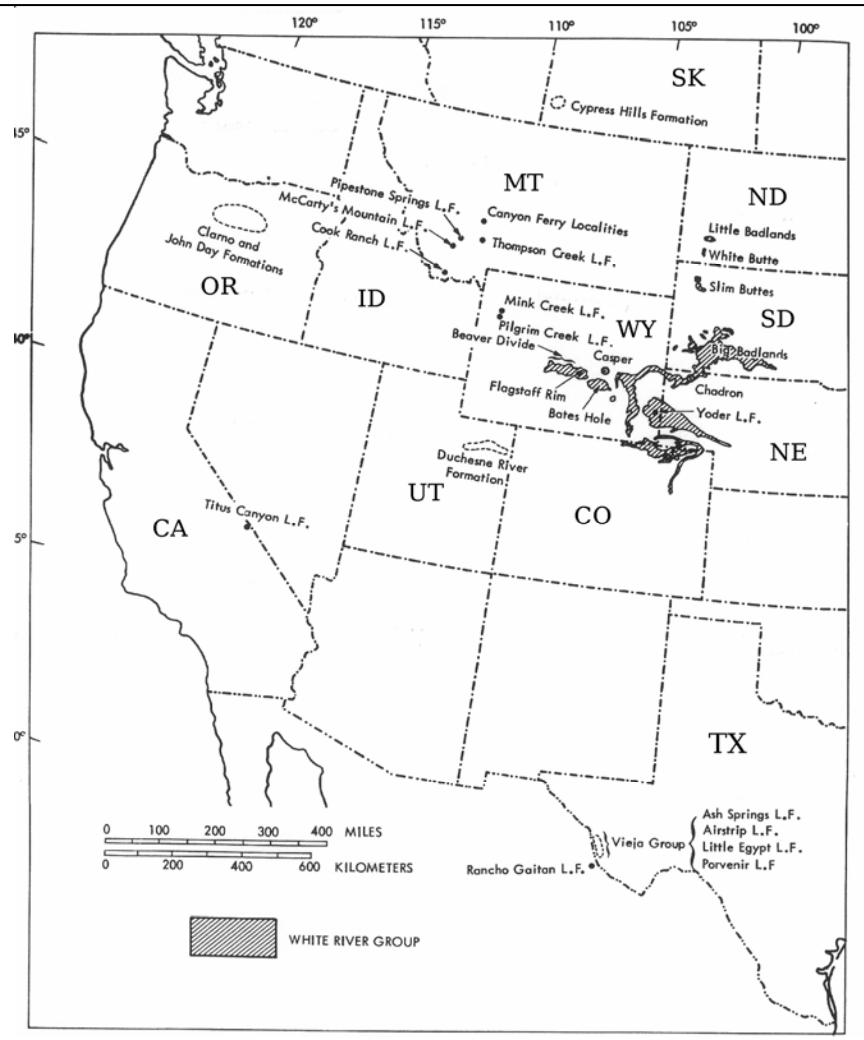


Figure 1.4. Map of the Chadronian, Orellan and Whitneyan localities of North America. Modified from Emry *et al*. (1987) by Rothecker (2003).

the Whitneyan were mostly stable, with some immigration and extinction events, but significant faunal changes that end the chronofauna began in the early Arikareean (Emry *et al.*, 1987).

Storer (1996) determined that the mammals of the Cypress Hills Formation indicated a close affinity with other Great Plains localities that were part of the White River Chronofauna, and should only have varied regionally based on local ecology. Recognition of this point was another leading cause for the re-evaluation of the NALMA of the Cypress Hills Formation, as some taxa were being described that were more advanced than would be expected in Chadronian-age sites. It is now understood that the anomalous taxa were a result of assuming that most Cypress Hills fossil localities represented the same NALMA age (Storer and Bryant, 1993).

Based on the recognition by Storer (1996) that the localities of the Cypress Hills Formation are part of the White River Chronofauna, the fossils from Rodent Hill can be correlated with other White River faunal assemblages within the White River Group. White River Group and other localities are shown in **Figure 1.4**. Correlation of the rodent families of this study requires comparison to sites of Orellan, Whitneyan and early Arikareean age (**Table 1.3**).

Table 1.3. Orellan, Whitneyan and early Arikareean sites in North America. From Emry *et al.* (1987) except where noted.

Orellan Localities

- Orella Member, Brule Formation – Nebraska, Wyoming
- Scenic Member, Brule Formation – South Dakota
- Cedar Creek Member, Brule Formation – Colorado
- Cedar Ridge Local Fauna, Badwater Creek area – Wyoming (Setoguchi, 1978; Korth, 1981)
- Cook Ranch and Matador Ranch Local Faunas, Cook Ranch Formation – Montana (Tabrum *et al.*, 2001)
- Climbing Arrow Formation – Montana
- Dunbar Creek Formation – Montana
- Renova Formation – Montana
- John Day Formation – Oregon
- Fossil Bush Locality and Anxiety Butte, Cypress Hills Formation – Saskatchewan (Storer, 1996)

Whitneyan Localities

- Whitney Member, Brule Formation – Nebraska, Wyoming
- Poleslide Member, Brule Formation – South Dakota
- Vista Member, Brule Formation – Colorado, South Dakota
- John Day Formation – Oregon
- I-75 Locality – Florida (Patton, 1969)
- ?White Hills Local Fauna, Blacktail Deer Creek Formation – Montana (Tabrum *et al.*, 2001)
- Rodent Hill Locality and Anxiety Butte, Cypress Hills Formation – Saskatchewan (Storer, 1996)

Early Arikareean Localities

- Gering Formation – Nebraska, South Dakota (Tedford *et al.*, 1996)
- Rockyford Ash Member, Sharps Formation - South Dakota
- John Day Formation – Oregon
- Mill Point Local Fauna, Grasshopper Basin – Montana (Tabrum *et al.*, 2001)
- Blacktail Deer Creek Formation – Montana (Tabrum *et al.*, 2001)
- Kealey Springs Local Fauna, Cypress Hills Formation – Saskatchewan (Storer, 1996)

1.5 OBJECTIVES

This study will analyze the rodent families Aplodontidae, Sciuridae, Castoridae, Heteromyidae, Florentiamyidae, Heliscomyidae and Zapodidae at the Rodent Hill Locality. The primary goal is to describe the rodent species present at Rodent Hill in the aforementioned families.

Once the rodent taxa are identified, objective one will be to test the Whitneyan age designation of the Rodent Hill Locality. Wood (1980) considered rodents an ideal group for biostratigraphy, and utilized them to correlate the Oligocene localities of North America. It is anticipated that comparisons of the Rodent Hill rodents, described herein, with taxa from other Orellan, Whitneyan and Arikareean localities, particularly from the Great Plains, will provide strong support in determining the age of Rodent Hill.

Objective Two is to test for any stratification of the rodent taxa throughout the Rodent Hill section. There is the possibility that a noticeable change in the rodent fauna could be present within the stratigraphy of the site, giving a better understanding of rodent evolutionary events in the age represented by the Rodent Hill Locality. Rodents of demonstrably different ages could also be present at Rodent Hill. This might involve different subdivisions within a NALMA age, or the recognition of more than one NALMA age within Rodent Hill.

Objective Three is to produce a more detailed sedimentological and stratigraphic description of the Rodent Hill Locality. This data will be used in determining any faunal stratification within the site.

Objective Four of this study is to present new information on the described rodent families, and augment the faunal characterization of the NALMA age determined for the Rodent Hill site. Based on the work of previous workers (Storer and Bryant, 1993; Storer, 1996; Rothecker, 2003) the working hypothesis will be that the Rodent Hill Locality probably represents a Whitneyan-age site, although the rodents found in this study might indicate otherwise.

A well-supported Whitneyan age designation would make this characterization particularly important, as Whitneyan age sites are very uncommon (Emry *et al.*, 1987) and small mammal faunas are especially rare (Setoguchi, 1978). Korth (1994a) listed only 15 species of rodent in the Whitneyan, compared to 48 in the preceding Orellan, and 110 in the ensuing Arikareean. Since 1994, there has been an increase in the described rodent taxa from the Whitneyan, but the diversity of Whitneyan rodents continues to appear far below that of most other ages. The low number of fossil-bearing Whitneyan sites is the cause of this apparent reduced diversity, rather than a real taxonomic plunge during the Whitneyan. This conclusion is borne out by the genera and even families of rodents that are present in the Orellan and Arikareean, but have not been recovered from the Whitneyan (Korth, 1994a). There has been the suggestion (Prothero and Whittlesey, 1998) that temporal ranges of many micromammal groups, particularly taxa with last appearances in the late Orellan, will be extended with increased discoveries of Whitneyan microfossil sites. The majority of the fossils from the Rodent Hill Locality are small mammal remains, with a high proportion of rodents. Rodent Hill has the potential to be a very important fossil site due to the abundance of small mammal fossils recovered there.

Of the families being studied here, some are better known from Whitneyan faunas than others. Korth (1994a) lists the Aplodontidae as the family with the most recognized taxa (6). There are two recognized species in the Sciuridae, and only one each from the Heteromyidae, Florentiamyidae and the Castoridae. There are no listed species in either the Heliscomyidae or the Zapodidae.

If there is support for the Whitneyan designation for Rodent Hill, this would be important for the refinement of Whitneyan biostratigraphy, which is currently defined primarily by larger mammals, including oreodonts, camelids and equids. The rodent taxa *Proheteromys nebraskensis*, *Agnotocastor praetereadens*, *Eumys brachyodus*, *Scottimus lophatus*, *Paradjidaumo* and *Ischyromys* were identified by Emry *et al.* (1987) as having the potential to be important to definitions of Whitneyan biostratigraphy. When Prothero and Whittlesey (1998) reevaluated the Orellan and Whitneyan, the rodents that were indicated as important to Whitneyan biostratigraphy included *Agnotocastor praetereadens*, *Oropyctis pediasus*, *Cedromus wilsoni*, *and Metadjidaumo* *hendryi, Paradjidaumo, Eumys* and *Scottimus*. More information on Whitneyan small mammal faunas will be necessary to evaluate their biostratigraphic significance.

2. GEOLOGY OF THE RODENT HILL LOCALITY

2.1 STRATIGRAPHY AND SEDIMENTOLOGY OF THE RODENT HILL LOCALITY

2.1.1 Surface Appearance of the Rodent Hill Locality

The surface exposure of the site is composed of unconsolidated sediments, primarily clays to fine sands, with pebbles and carbonate nodules present throughout the section in varying abundance. The weathered surface of the site has been split into three distinct surface features that have generally been referred to when the site is described in unpublished field notes. The bottom-most portion is light buff color; the top portion is gray. Both of these layers are composed of the clays to fine sands that typify the Rodent Hill Locality. Between the two different-colored layers is a prominent bench that is more resistant to weathering than either the top or bottom layers. The sediment of the bench is predominantly fine to medium sand with a much higher relative proportion of calcrete. These nodules are generally larger and contain more sand-size material than the other nodules from the site. The surficial appearance of the two unconsolidated layers is due to erosion and deflation of the site, whereas the bench appears be a relatively stable feature.

2.1.2 Stratigraphy and Sedimentology of the Rodent Hill Locality

In the summer of 2001 the author, with Harold Bryant, sampled the Rodent Hill Locality stratigraphically. The side of the hill was dug out as steps so that a clear vertical column of the locality would be visible without the loose overburden obscuring the stratigraphy (**Figure 2.1**). The sedimentary features indicate a more complicated lithostratigraphic sequence than previously recognized from the surface exposure.

Figure 2.1 The Rodent Hill Locality. A step trench being dug out of Rodent Hill in 2003. The "bench" (indicated by arrow) is visible as a light horizontal line to the left of the trench, with plants growing directly above it. The distinction in the color of the upper and lower surface layers has been obscured

The site was then divided into seven stratigraphic units based upon the sediments and sedimentary structures. Samples were dug directly from Units I and II at the bottom of the section, and from Units V, VI and VII at the top (**Figure 2.2)**. The assumption was that any faunal shifts that were present at the site would be most obvious between the furthest apart units.

The base of the section is a contact with an unstudied unit that is well below the level of the road beside the locality and was not dug out except to determine the base of Unit I. The sediment below Unit I is compact medium-coarse sand that is not cemented, and contains a large number of calcrete and clay nodules. No samples were taken from this unit for this study.

The lowest unit, Unit I, is one of the thickest units (180 cm), composed of fine sand and silt-sized laminae primarily present as cross-laminated ripples, although some are more planar. Throughout the layer there are local short, very thin lenses composed

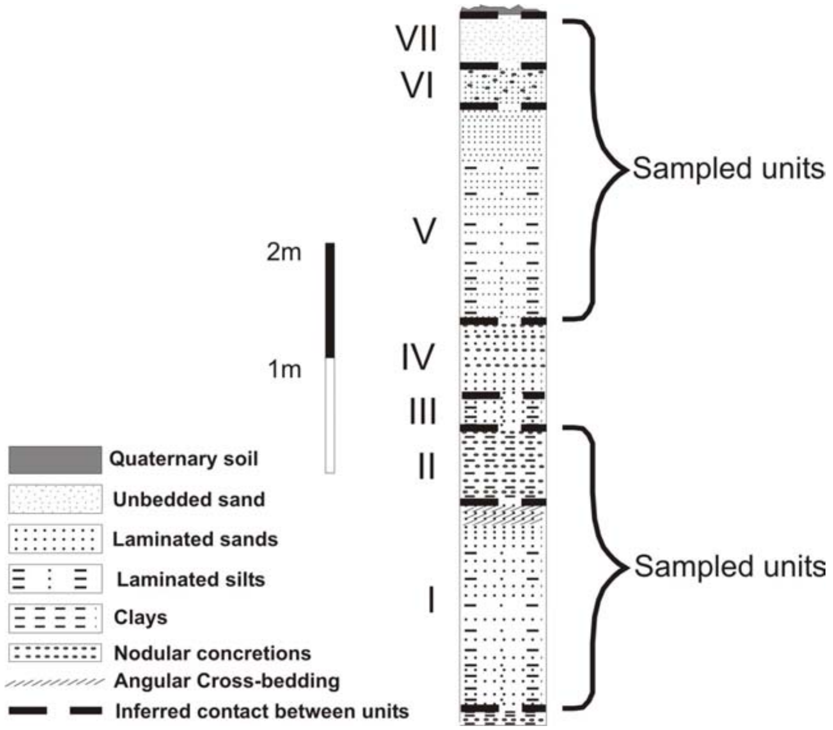


Figure 2.2. Stratigraphic column of Rodent Hill sedimentary units.

of clay intraclasts. At the bottom of this unit the laminae of silts and sands are about equal in number and thickness, while the unit coarsens at the top to be predominantly sandy laminae. This unit was the most fossiliferous of the sampled units.

Unit II is the nodular bench that is clearly visible on the weathered surface of the Rodent Hill Locality. It is about 68cm thick. The nodules here are composed mainly of calcrete and are relatively large, up to pebble size. There is some sand within the layer, but for the majority of the unit all interstitial clastics have been weathered away. The dominance of the nodules gives this unit the resistance to weathering that produces the surficial bench feature that has been used to separate the top and bottom of the Rodent Hill Locality. Fossils were obtained from this unit, but not nearly as many as produced in Unit I.

Unit III is roughly 25 cm thick and primarily composed of sand and silt angular cross-laminations. Throughout this unit there are numerous clay intraclasts. The origin of these clasts is currently unclear. Unit III was not sampled for fossils.

Unit IV is approximately 65 cm thick, and has a more complicated structure than the other units. The lower part of this unit has some large calcrete nodules, several centimeters long, in an unsorted sand matrix. They appear to have formed *in situ* and were probably not transported. In the middle of the unit the sediment is also composed of large amounts of sand matrix, with smaller clay clasts and calcrete nodules throughout. The top of the unit is similar to Unit II, with very little sand present and a predominance of mostly horizontal silcrete nodules that form a layer that is more resistant to weathering than the sandy units. Unit IV also was not sampled for fossils.

Unit V is the thickest unit (187 cm) and is composed primarily of interbedded sands and silts with only a few clay nodules present in small accumulations. This was the second-most fossiliferous unit, although many fewer teeth were recovered here than from Unit I.

Unit VI is a thin unit, 36 cm thick that is very similar to Unit II, with some sand matrix and a predominance of silcrete nodules forming a weathering-resistant layer. This unit was sampled for fossils, but only three teeth were recovered, and very few bone fragments compared to the other sampled units.

Unit VII is the top unit, 45 cm thick, composed primarily of massive medium-size sands. This unit was sampled for fossils, and while relatively few fossils were recovered, some were of direct interest to this study due to their relatively advanced nature.

2.2 DEPOSITION OF THE RODENT HILL LOCALITY

The sedimentology of the Rodent Hill Locality units may indicate an intermittent stream of the kind proposed by Leckie and Cheel (1989) to explain the deposition of the Cypress Hills Formation. The laminated and cross-bedded fine sand grains indicate fluvial movement from a western direction. The amount of time to deposit this material is unknown. The layers that are composed primarily of nodules likely signify periods when the area was drier. These nodules normally take hundreds to thousands of years to form (Leckie and Cheel, 1989; 1990) and there is no reason to believe that this would be different at the Rodent Hill Locality. These nodules could have formed from the precipitation of minerals from the local groundwater. High amounts of precipitation or other sources of water might have encouraged the minerals to move back into solution; therefore, long periods of time between events of high amounts of moisture (precipitation or inundation) are likely. However, smaller amounts of moisture in the area are possible, and would not have impeded the formation of the calcrete nodules. Once formed as resistant layers these units would have provided surfaces for later fluvial deposits when streams did flow in the area. Evidence for this is the scoured upper surfaces of the nodular layers. The alluvium that was present on top of the nodular layers could have been scoured away and new alluvium deposited several times until there was finally a long enough hiatus that left a fluvial deposit in place. With time, new nodular horizons would form at the top of the fluvial deposit, repeating the cycle.

The source for the Cypress Hills Formation was determined to be from the uplift and erosion of the Sweetgrass Hills and Bearpaw Mountains in western Montana (described above) (Leckie and Cheel, 1989). There is no reason to believe that the Rodent Hill sediment did not share this provenance. The one deposited structure that is found at Rodent Hill that could not have come from Montana are the small clay intraclasts that are found throughout the fluvial sections. These structures are generally small, less than 3 cm, and are very friable. They are also generally round in shape, and are therefore products of transport. A likely source for this clay would be earlier-aged sites in the Cypress Hills. At the nearby Bud Locality there is a large amount of clay in some layers that appears very similar to the clay in the balls found at Rodent Hill, offering a probable source for these sediments (Leckie and Cheel, 1989). It is fortunate that fossils are only rarely recovered from these clay layers in that Chadronian-age site, so that it is unlikely that a Whitneyan fauna at Rodent Hill has become mixed with an earlier Chadronian one. The fossil rodents recovered at Rodent Hill also bear this out.

Leckie and Cheel (1989) describe the Saskatchewan portion of the Cypress Hills as the product of a braid plain or meandering stream plain that flowed in a semi-arid region. The Rodent Hill Locality appears to reflect a similar depositional situation, with the locality possibly occurring at the edge of the flood plain. If this were the case, the sand bars (Units I, III, V and VII) would form during episodes where the stream flowing from the southwest had shifted northward, depositing the alluvium. The nodular units

(II, IV, and VI) would have formed during the longer periods when the stream was not in a position to deposit large amounts of water and alluvium into the area while the silcretes consolidated. One factor that is unknown, and at this time untested, is how much time is missing in the disconformity between the consolidation events of the nodular units and the deposition events of the sand bars. This period of time could be nil, *i.e.*, the sand bars indicate a direct deposition immediately after the formation of the nodular units. Conversely, there could be hundreds or thousands of years indicated by the time between the solidification of the nodules and the sand deposits. This question currently remains unresolved.

Another important consideration is the mixing of faunas during transport. There is the potential that the streams that deposited the Rodent Hill fossils during one NALMA were also cutting down into older sediment, thus combining species of different ages. At the Rodent Hill Locality there is no definite way to know for sure, but there are no described taxa that stand out as anomalous in age compared to the rest. Based on the evidence from this study, the possibility must be considered for the combining of faunal elements from different ages due to stream action, but is unlikely to have had much effect on the mammal remains at the Rodent Hill Locality.

3. METHODS AND MATERIALS

3.1 MATERIALS – FOSSILS USED IN THIS STUDY

The fossils for this study were recovered from two sources. The first was the non-stratigraphically controlled materials that had been previously collected from the Rodent Hill Locality by other workers. The collection of many of these specimens came from surface collecting or sorting through matrix. Some fossils were obtained by picking through matrix that was collected in 1994. The specimens that were recovered by other people had been catalogued and given RSM P-numbers (**Table 3.1**), and some had preliminary familial identifications, but only one relevant specimen, P2785.021, had been identified to the species level. This specimen was identified as the aplodontid *Prosciurus relictus* (Storer, 1993), a species found elsewhere in Orellan sites only (Korth, 1989a) so the Whitneyan age assignment of Rodent Hill needed to be tested. It also became apparent that it would be important to test if there was an identifiable stratification of taxa within the site, in order to determine whether material of an older (likely Orellan) or younger (likely Arikareean) age might be identified from a distinct layer.

Sediment that was collected by using a shovel was processed in a double-drum power screen. The amount of sediment screened from each of the units varied, but at least 100 liters were removed from all units except Unit VI, for which 50 liters was screened. The volume of screened material was determined by the volume of the

Table 3.1. RSM P-numbers of non-stratigraphically collected fossils and the total number of rodent teeth in this study assigned to each P-number.

P number	2452	2521	2685	2706	2785	2794
Number of rodent teeth	20	105	1	2	2	1

available containers, each of which was about 45 L. Each unit produced a similar volume of screened matrix (the screened material of Unit VI produced a similar volume after screening only half the amount taken from the other stratigraphic units).

The power screen was used to remove all of the very finest (<1 mm) sediment and to separate the coarsest material (>5 mm) from the rest of the sediment. There was the possibility that the very tiniest of fossils, such as insectivore incisors and reptile teeth, could be lost in the clays and silts that were left behind. These elements were recovered from the sampled matrix from this site and others in the Cypress Hills, so considering the costs versus the benefits, the potential to miss a few small fossils was considered minimal compared to the amount of time that would have to be expended sorting through the voluminous amounts of clays and silts.

The two separate sets of samples were then brought back to the University of Saskatchewan to be sorted. The search for fossil material was accomplished by placing a small amount of matrix on a tray, then picking out fossils with fine forceps under a magnifying lamp. All fossil material was retained, including teeth, skeletal elements and fragmentary remains. Only the teeth, and mandibles and maxillae with teeth present, were collected in individual containers and assigned individual catalogue numbers (except for rodent and lagomorph incisors). The rest of the fossils were placed in containers, one containing skeletal elements and the other containing fragments. The fossils from each unit were assigned a different RSM "P" number to avoid later confusion (**Table 3.2**).

Table 3.2. P-numbers assigned to Stratigraphic Units of Rodent Hill, total number of associated dental remains, and the total number of rodent teeth relevant to this study (excludes eomyids and cricetids).

Stratigraphic Unit	I	II	III	IV	V	VI	VII
P number	P2834	P2835	N/A	N/A	P2836	P2837	P2838
Total dental remains	165	28	0	0	37	3	15
Total rodent teeth	15	6	0	0	9	0	5

After the matrix had been sorted, a process that took approximately one year, the dental remains were then sorted and identified to taxonomic group. The rodents from the families involved in this study were assigned tentatively to families; the cricetids and eomyids were passed on to another researcher (Jennifer Rothecker), who was working on those two families.

3.2 METHODS - COMPARISONS AND IDENTIFICATIONS

The fossils for this study were recovered from either the stratigraphic samples or from previous collections at Rodent Hill. The fossil material from the rodent families of interest was sorted and identified to the most specific taxonomic level possible, depending on the nature of the collected fossils and the comparative material available. The teeth were first sorted into appropriate families based on literature descriptions of the families, and some were tentatively assigned to genera where possible. Once sorted into families, the teeth were measured using a Nikon eyepiece reticule in a Leitz dissecting microscope.

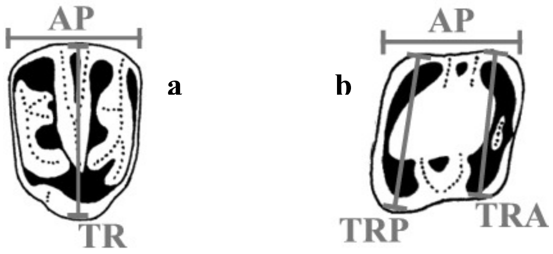


Figure 3.1 Occlusal measurements used for all rodent teeth. **a.** Upper tooth (M1); **b.** lower tooth (m1). Redrawn from Meyer, 2003.

The occlusal surface of each tooth was measured for the maximum anteroposterior length (**AP**), and the maximum transverse width (**TR**) whenever possible (**Figure 3.1a**). In the case of lower teeth (**Figure 3.1b**), each was measured for the maximum transverse width across both the trigonid (**TRA**) and the talonid (**TRP**). Castorid teeth (**Figure 3.2**) were also measured for maximum lingual and buccal enamel height (**LEH** and **BEH**, respectively). Upper teeth are designated using upper case

Figure 3.2 Lateral enamel measurements of castorid dentition. Redrawn from P2685.002 (RP4), buccal to left.

letters, followed by a number that indicates the tooth position in the row (e.g. P4, M1). Lower teeth are indicated using lower case letters (e.g. p4, m1).

The measurements were plotted into Excel spreadsheets for comparisons on scatter plots so that distinct taxa could be recognized based on sizes, and any trends in measurements would become apparent, allowing for further sorting of the fossils. Where more than one specimen in a tooth position was known for a taxon, the **MEAN** of the measurements is calculated and the operational range of sizes (**OR**) are given to indicate minimum and maximum measurements. Where four or more specimens were known, the standard deviation (**SD**) and coefficient of variation (**CV**) were calculated.

At this point, it became necessary to compare the Rodent Hill fossils with similar fossils from other localities. Specimens were borrowed from collections at other institutions whenever possible for direct comparison. A trip to the American Museum of Natural History was considered necessary because of the relatively large number of relevant holotypes present there that could not be borrowed. In this case, photographs were taken using a Kodak DX3900 3.1MP digital camera. In other cases, casts of holotypes were provided while paratypical material was borrowed. When necessary, the Rodent Hill fossils were compared with literature descriptions and figures if the comparative material was not available for loan.

Specimens were referred to taxa based on shared morphological similarities with known material. In a few cases the fossils were unlike any that have been described, in which case they were considered a new species. In some instances this resulted in the diagnosis and naming of a new species. In other instances, the material was identified as unique, but no specific designation was given. The choice in such cases depended on the amount of material present, the condition of the material, and completeness of the resulting upper and lower dentitions.

4. RODENT OVERVIEW

4.1 SPECIALIZED STRUCTURES OF RODENTS

The rodents are a large order of mammals with several specializations in their dentition and skulls related to their unique form of mastication called propalinal movement (Carroll, 1988, p. 489) that involves an anteroposterior motion of the jaw. Some of these cranial and dental adaptations are used in the taxonomy within the order. They are introduced here to avoid detailed discussion in the following chapters on the families, and will focus on two particular skull features, and the dentition. The zygomatic structure and jaw angle are discussed here, as they are skull characteristics that are commonly used to group rodents at higher taxonomic levels, while the unique dentition of rodents can be used to distinguish between genera or species.

4.1.1 Zygomasseteric Structure

The muscles that rodents use for chewing are adapted to allow the jaw to move in a back-and-forth motion. To accomplish this, the masseter muscle is differentiated into three parts and extends anteriorly onto an extended zygomatic arch that originates anterior of the tooth row (Korth, 1994a). The masseter muscle extends between the ventral surface of the zygoma and the lateral side of the ascending ramus (Korth, 1994a).

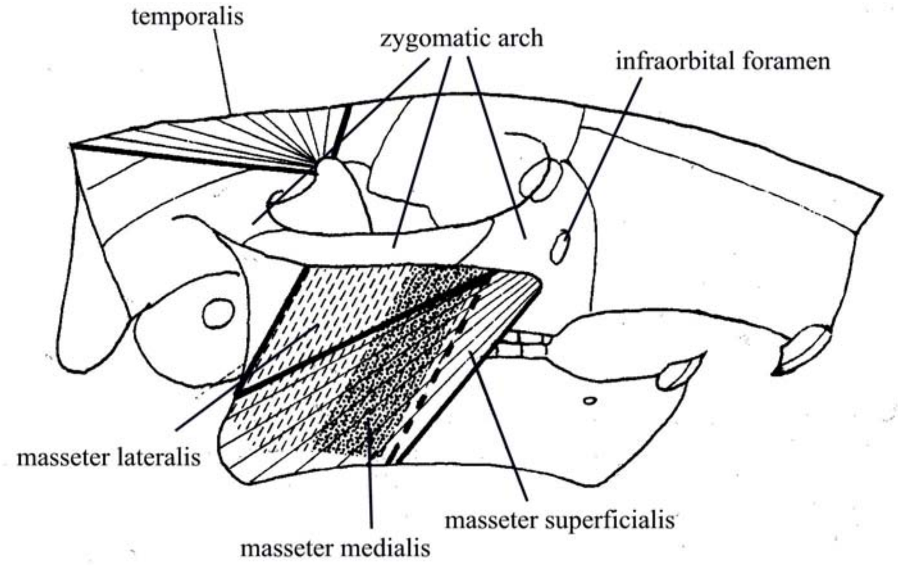


Figure 4.1 The major muscles of rodent mastication and the skull structures relevant to the morphology of the zygomatic arch. Modified from Korth, 1994a.

The zygomasseteric structure of the skull is arranged in four different ways in rodents, which allows for variations in the expansion of the various masseter muscles onto the rostrum (Korth, 1994a). These morphologies are used in subordinal classifications of the rodents, and are known as protrogomorphy, sciuromorphy, hystricomorphy and myomorphy (**Fig. 4.2**). These terms are used to describe variations in the modifications of the rostrum that may relate to an expansion of the anterior margin of the zygomatic arch into a plate, an increase in the size of the infraorbital foramen, or a combination of these.

4.1.1.1 Protrogomorphy

This is the primitive condition in rodents, where the rostrum is not modified, so the masseter originates only on the ventral surface of the zygomatic arch (Korth, 1994a). In the Rodent Hill rodents, this condition is seen in the Aplodontidae, the only modern family that still exhibits this condition (Korth, 1994a).

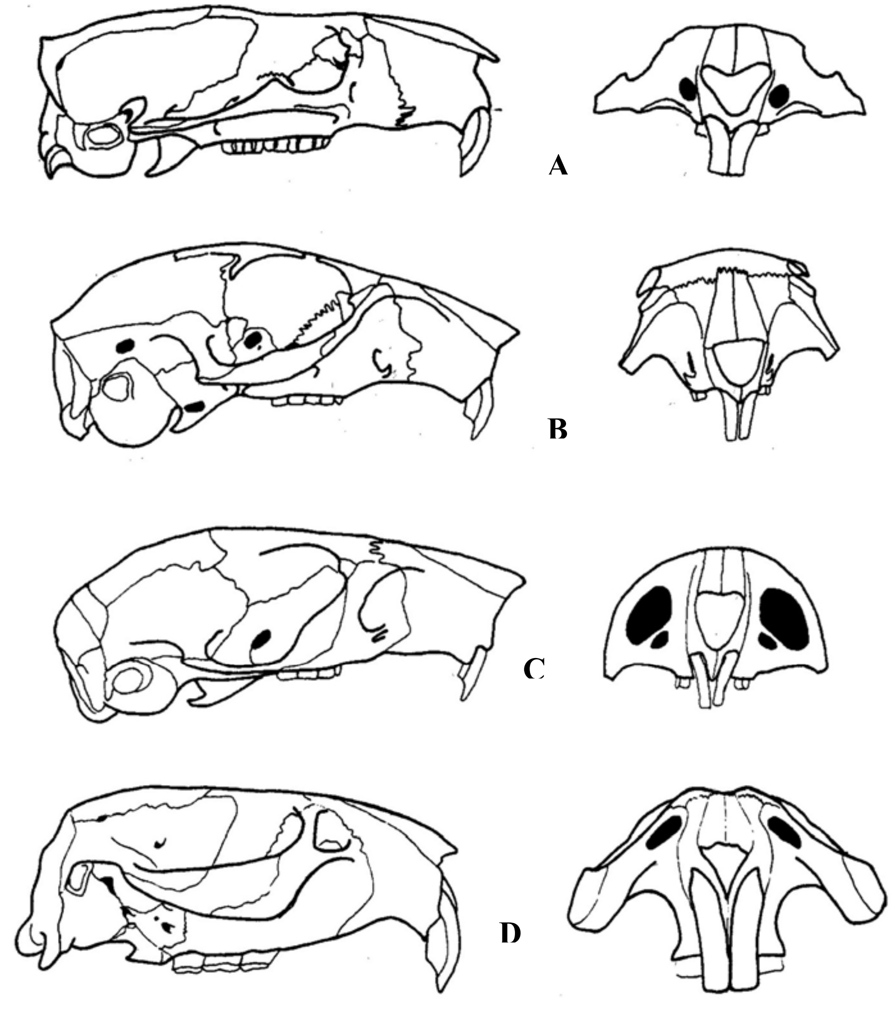


Figure 4.2 Examples of the four kinds of zygomasseteric structure in Recent rodents. **A**, Protrogomorphous *Aplodontia rufa*. **B,** Sciuromorphous *Sciurus niger*. **C,** Hystricomorphous *Zapus hudsonicus*. **D.** Myomorphous *Rhizomys pruinosis*. Skulls are not to scale. Modified from Korth, 1994a.

4.1.1.2 Sciuromorphy

This is a modification where the ventral surface of the zygoma tilts vertically and broadens into a zygomatic plate (Korth, 1994a). The masseter lateralis extends anteriorly onto the rostrum, while the m. superficialis extends anteriorly along the zygoma and the origination of the m. medialis is the same as in protrogomorphy (Korth, 1994a). Most of the Sciuridae, the Castoridae, and the families of the Geomyoidea are Rodent Hill families with this morphology. The Eomyidae, described by Rothecker (2003), are also sciuromorphous (Korth, 1994a).

4.1.1.3 Hystricomorphy

This is a condition where the masseter medialis is enlarged and passes through the infraorbital foramen, which is also enlarged (Korth, 1994a). The m. superficialis originates on the anterior edge of the zygoma, while the m. lateralis extends over most of the length of the zygoma (Korth, 1994a). The Zapodidae is the only Rodent Hill family of rodents in this study that express this morphology (Korth, 1994a). Some members of the Cricetidae, which were described by Rothecker (2003), are also hystricognathous (Korth, 1994a).

4.1.1.4 Myomorphy

This condition is a combination of the expansion and tilting of the zygoma to accommodate the masseter lateralis as seen in sciuromorphy, and the enlargement of the infraorbital foramen to allow for the m. medialis as in hystricomorphy (Korth, 1994a). None of the Rodent Hill rodent families in this study have this morphology, although Korth and Emry (1991) suggested that the sciurid subfamily Cedromurinae might have some myomorphic modifications. Some rodents of the family Cricetidae are also myomorphic (Korth, 1994a; Rothecker, 2003).

4.1.2 Angle of the jaw

The angle of the mandible relative to the horizontal ramus of the jaw is often used for subordinal classification of rodents (**Fig. 4.3**). There are two different morphologies: **sciurognathy**, where the angle of the mandible is in the same plane as that of the horizontal ramus, in a roughly straight line; and **hystricognathy**, where the horizontal ramus is at an angle to the mandible, giving a line with a distinct bend (Korth, 1994a). Some confusion does exist about these conditions in extinct taxa due to qualifications such as "incipient" or "subhystricognathous", and this may require recognition of an intermediate morphology that was able to evolve into either form (Korth, 1994a). All of the Rodent Hill rodents, including the Cricetidae and Eomyidae studied by Rothecker (2003), exhibit the sciurognathous condition (Korth, 1994a).

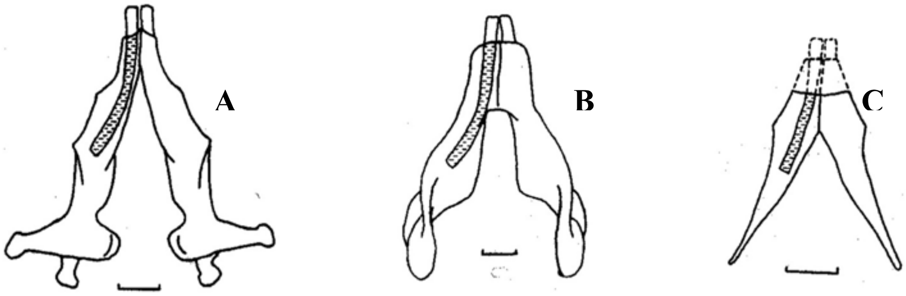


Figure 4.3 Jaw angle morphology in rodents. **A,** Sciurognathous *Aplodontia rufa* (Recent). **B,** Hystricognathous *Erethizon dorsatum* (Recent). **C,** "subhystricognathous" *Franimys amherstensis* (Clarkforkian). Scale equals 1 cm. Modified from Korth, 1994a.

4.1.3 Dentition

The primitive dentition of the Rodentia is 1023/1013 (Korth, 1994a) although this dental formula has been modified in several groups. The teeth of primary importance in this study are the cheek teeth (molars and premolars). Most of the dental homologies and terminology of rodents were summarized by Wood and Wilson (1936), and these are generally the terms used to describe the features of the teeth, although they have been modified by other authors to suit the special modifications found in many rodent families.

Figures **4.4** and **4.5** show generalized cusp and feature orientations of rodent molars and premolars. The basic occlusal pattern of the upper molars (**Figure 4.4**) is a triangle outline with a tribosphenic cusp pattern. There is a paracone and metacone on the buccal side, and a protocone on the lingual side. A hypocone may be present posterior to the protocone. On the anterior margin, a raised anterior cingulum may be present. Posterior to the anterior cingulum is a valley that is referred to as the anterior transverse valley. A protocone crest may extend buccad from the protocone into the anterior transverse valley. There are two main transverse lophs within the basin of the tooth that may be present; the protoloph is the anterior loph, usually extending linguad from the paracone to the protocone, while the metaloph is the posterior loph, extending linguad from the metacone towards the protocone. The valley between the two transverse lophs is called the central transverse valley. A protoconule may be present on the protoloph, and one or more metaconules may be present on the metaloph. On the

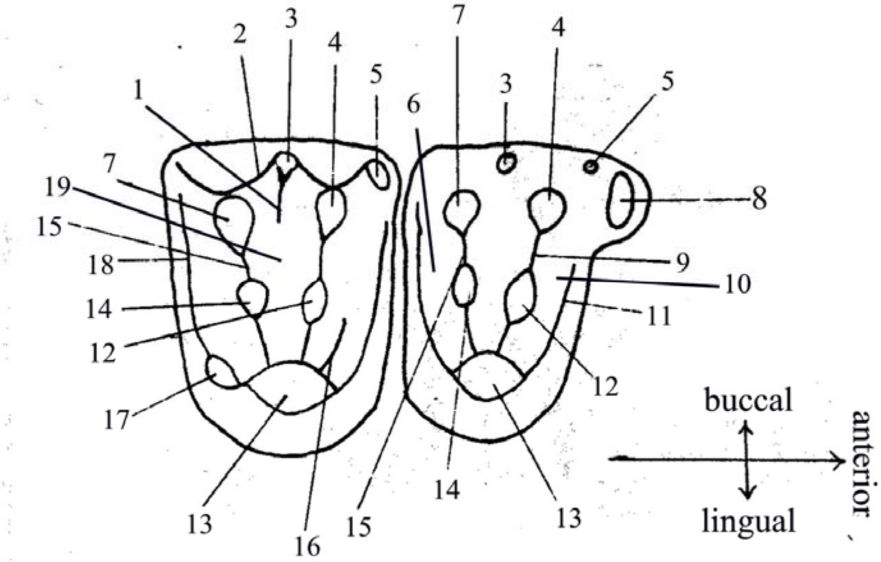


Figure 4.4 Generalized upper rodent molar (left) and premolar with major features identified. 1–mesostylar crest 2—ectoloph 3—mesostyle 4—paracone 5—parastyle 6—posterior transverse valley 7—metacone 8—anterocone 9—protoloph 10—anterior transverse valley 11—anterior cingulum 12—protoconule 13—protocone 14—metaconule 15—metaloph 16—protocone crest 17—hypocone 18—posterior cingulum 19—central transverse valley

Modified from Korth, 1994a.

posterior margin a raised posterior cingulum may be present. The valley between the metaloph and posterior cingulum is the posterior transverse valley. On the buccal margin, stylar cusps may be present; the parastyle is present anterobuccally to the paracone, while the mesostyle is present between the paracone and metacone. A mesostylar crest may extend lingually or buccally from the mesostyle. The ectoloph is a buccal loph that may join some or all of the buccal cusps.

The P4 is generally similar to the molars, but the anterobuccal corner may be expanded into an anteriorly oriented anterocone.

The lower molars (**Figure 4.5**) are roughly square in occlusal outline, and are divided into the anterior trigonid region and the posterior talonid region. The trigonid of rodents has two main cusps, the buccal protoconid and the lingual metaconid, and an anteroconid may be present in front of these two cusps. The loph that extends between

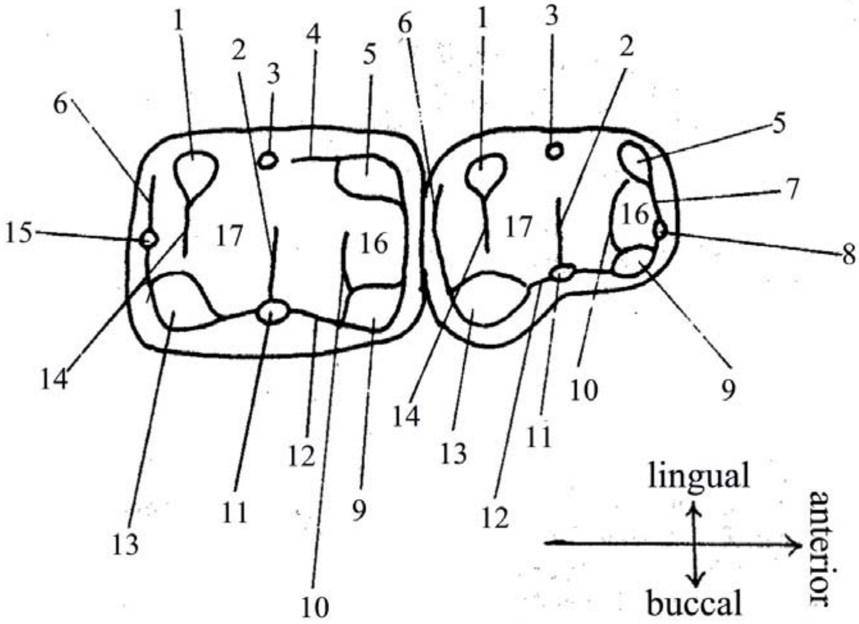


Figure 4.5 Generalized lower rodent molar (left) and premolar with major features identified. 1–entoconid 2—mesolophid 3—mesostylid 4—metastylar crest 5—metaconid 6—posterolophid 7—metalophulid I 8—anteroconid 9—protoconid 10—metalophulid II 11—mesoconid 12—ectolophid 13—hypoconid 14—hypolophid 15—hypoconulid l6—trigonid 17—talonid

Modified from Korth, 1994a.

the anterior margins of the protoconid and metaconid is the metalophulid I (=anterior cingulum of Korth, 1994a) and the loph that extends between the posterior margins of those cusps is the metalophulid II. This latter loph may not completely traverse the width of the trigonid, instead leaving the posterior margin of the trigonid basin open. Posteriorly, there are three main cusps of the talonid, the hypoconid on the posterobuccal corner, the entoconid on the posterolingual corner, and a hypoconulid between those two cusps. The loph that extends along the posterior margin, joining these cusps, is the posterolophid (=posterior cingulum of Korth, 1994a). The hypolophid is a loph, present anteriorly to the posterolophid, that extends between the hypoconid and entoconid; this loph may be complete, joining the two cusps, or may be incomplete. On the buccal margin of the tooth, an ectolophid may be present as a crest that runs posterad from the protoconid to the hypoconid. A mesoconid may be present as a small cusp along the ectolophid. On the lingual margin, a metastylid crest may extend posterad from the metaconid. This crest may or may not extend to join with the entoconid, or it may terminate at one or more mesostylid cusps that are present on the lingual margin.

The lower premolar has most of the same features of the lower molars, but the talonid is usually buccally expanded relative to the trigonid (Korth, 1994a) although this may occur in the lower molars of some taxa as well.

Many rodent families can be identified due to modifications of this general tooth morphology; distinguishing features will be indicated within each family discussion. Many genera and species of rodents are diagnosed solely on their dental structure *e.g. Sciurion campestre* Skwara, 1986; *Pseudallomys nexodens* Korth, 1992; *Nototamias* Pratt and Morgan, 1989. This allows for identification of the rodents from Rodent Hill even though the majority of identifiable dental remains recovered from the site are isolated teeth.

4.2 THE RODENT FAMILIES OF RODENT HILL

The following families of rodents were identified from Rodent Hill Locality. The taxonomy follows that of Korth (1994a), as it is the most recent review of the systematics and diversity of the Tertiary rodents of North America. McKenna and Bell (1997) is a more recent classification of the all of the mammals, including alternate classifications of the rodents, but the rodent-specific nature of Korth makes it the preferred source here.

- Order Rodentia Bowditch, 1821
  - Suborder Sciuromorpha Brandt, 1855
    - Superfamily Aplodontoidea Brandt, 1855
      - Family Aplodontidae Trouessart, 1897
    - Superfamily Sciuroidea Gray, 1821
      - Family Sciuridae Gray, 1821
  - Suborder Sciuromorpha *incertae sedis*
    - Superfamily Castoroidea Gray, 1821
      - Family Castoridae Gray, 1821
  - Suborder Myomorpha Brandt, 1855
  - Infraorder Myodonta Schaub, 1958
    - Superfamily Muroidea Miller and Gidley, 1918
      - Family Cricetidae Rocheburne, 1883
    - Superfamily Dipodoidea Weber, 1904
      - Family Zapodidae Coues, 1975
  - Infraorder Geomorpha Thaler, 1966
    - Superfamily Geomyoidea Bonaparte, 1845
      - Family Heteromyidae Gray, 1868
      - Family Florentiamyidae Wood, 1936
      - Family Heliscomyidae Korth Wahlert and Emry, 1991
    - Superfamily Eomyoidea Depéret and Douxami, 1902
      - Family Eomyidae Depéret and Douxami, 1902

5. FAMILY APLODONTIDAE

The Aplodontidae is considered the most primitive living family of rodents, containing the single living species, the mountain beaver or sewellel *Aplodontia rufa* (Korth, 1994a) that has a range limited to the northwest United States and southern British Columbia.

The earliest aplodontids are known from isolated teeth from the Uintan and Duchesnean (Black, 1971; Storer, 1988) and indicate a likely origin within the rodent family Ischromyidae (Korth, 1994a). Aplodontids were at a peak of diversity during the Arikareean (Korth, 1994a) and decline rapidly after that. During the Oligocene and early Miocene the family has a fossil record that is rare, but diverse, in Europe and Asia as well as in North America (Korth, 1994a).

The Aplodontidae is the only living rodent family that still bears the primitive protrogomorphic zygomasseteric structure, and the jaw angle is sciurognathous (Korth, 1994a).

The dental formula of aplodontids is the primitive rodent formula of 1023/1013 (Korth, 1994a). The basic upper molar morphology (**Figure 5.1**) of the aplodontids is a brachydont tooth with large conules, a mesostyle that would develop into an ectoloph in some lineages, protocone crest and reduced hypocone (Korth, 1994a). The P4 is often larger than the M1, usually with an expanded anterocone (Korth, 1994a).

The basic lower molar morphology of aplodontids (**Figure 5.2**) has a hypolophid (partial or complete), and an entoconid that is distinctly isolated from the posterolophid (Korth, 1994a). The p4 is molariform with a trigonid that is constricted relative to the talonid (Korth, 1994a).

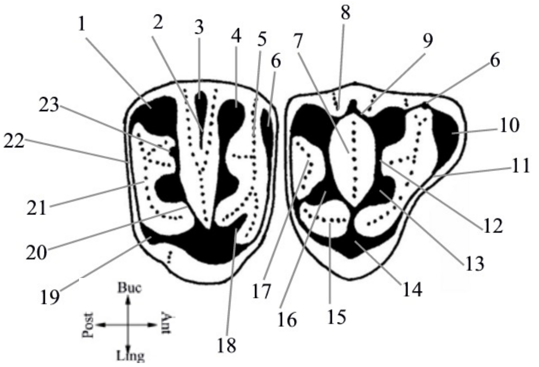


Figure 5.1 Generalized aplodontid upper cheek tooth morphology. RM1 (on left) and RP4 with major features identified. 1–metacone 2—metastylar crest 3—mesostyle 4—paracone 5—anterior transverse valley 6—parastyle 7—central transverse valley 8—buccal (=labial) fossette 9—ectoloph 10—anterocone 11—anterior cingulum 12—protoloph 13—protoconule 14—protocone 15—posterior lingual inflection 16—metaconule (=lingual metaconule) 17—posterior labial fossette 18—protocone crest 19—hypocone 20—metaloph 21—posterior transverse valley 22—posterior cingulum 23—second metaconule (=buccal metaconule)

Drawn by Taran Meyer, modified by the author. Terminology from Wood and Wilson (1936) and Rensberger (1975).

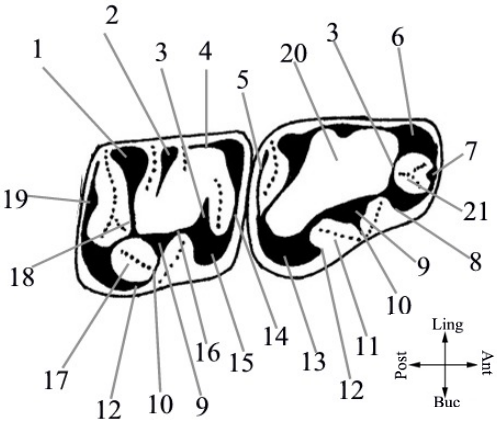


Figure 5.2 Generalized aplodontid lower cheek tooth morphology. Rm1 (on left) and Rp4, with major features identified. 1—entoconid 2—mesostylid 3—metalophulid II 4—metastylid crest 5—posterolophid (=posterior cingulum) 6—metaconid 7—anteroconid 8—posterior protoconid crest 9—mesoconid 10—buccal mesolophid 11—metastylar (buccal) shelf 12—anterior hypoconid crest 13—hypoconid 14—metalophulid I (=anterior cingulum) 15—protoconid 16—ectolophid 17—posterior buccal fossettid 18—hypolophid 19—hypoconulid 20—talonid 21—trigonid

Drawn by Taran Meyer, modified by the author. Terminology from Wood and Wilson (1936) and Rensberger (1975).

Crown heights of aplodontids are primitively brachydont, as in the subfamilies Prosciurinae and Allomyinae, but there is a trend toward greater hypsodonty in the later subfamilies Meniscomyinae and Aplodontinae (Korth, 1994a). The subfamilies found at Rodent Hill, the Prosciurinae and the Allomyinae, can be differentiated dentally by the relative complexity of the cheek teeth. Prosciurines have teeth dominated by cusps, with fewer lophs and crests (Korth, 1994a) whereas the teeth of allomyines are more complex, with more lophules and crests.

5.1 SYSTEMATIC PALEONTOLOGY

APLODONTIDAE Trouessart, 1897

PROSCIURINAE Wilson, 1949

PROSCIURUS Matthew, 1903

Type species—*Sciurus vetustus* Matthew, 1903

Referred species—*P. relictus* (Cope, 1873); *P. lohiculus* Matthew and Granger, 1923; *P. shantungensis* Rensberger and Li, 1986; *P. ordosicus* Wang, 1987; *P. parvus* Korth, 1989b; *P. magnus* Korth, 1989b; *P. albiclivus* Korth, 1994b.

Age and distribution—Chadronian, Orellan of Great Plains of North America, Whitneyan of Nebraska and Saskatchewan, Oligocene of Mongolia and China, questionably Arikareean of Saskatchewan.

Diagnosis—"Small, brachydont aplodontids lacking ectoloph in P^4-M^3; distinct protoconule (paraconule) on P^4-M^3 that may be reduced in the smallest species; metaconid anteroposteriorly compressed, allowing extension of deep interior basin farther anterolinguad than in other genera; metalophulid II absent on metaconid, present on protoconid; mesostylid separated from metaconid, lacking transverse compression; mesostylid with tendency to bear small, transversely directed crest, either bending posterad toward hypoconulid, or bending towards ectolophid, often joining posterior corner of mesoconid." Diagnosis of Rensberger (1975) emended by Korth (1989).

PROSCIURUS CF *P. PARVUS* Korth, 1989b

Table 5.1, Figure 5.3 a-c

Type specimen—UNSM 81084, left mandible with m1-m2, Brule Formation, Morrill County, Nebraska (Orellan).

Referred specimens—SMNH P2521.154 (LP4); P2785.021 (RM1); P2521.321 (LM1); P2452.121 (LM?); P2521.305 (Lp4).

Horizon at Rodent Hill—Collected in stratigraphically uncontrolled sampling.

Diagnosis—"Smallest species of the genus; metaconules on upper molars single; hypolophid on lower cheek teeth less well-developed than that of *P. relictus*; mesostylid strong and buccolingually elongate on lower molars; minute cingulum variably present at posterior base of protoconid." From Korth (1989a).

Description—The P4 has an anteroposteriorly-compressed anterocone with a parastyle situated buccally. The anterior transverse valley is wide between the anterocone and protoloph, and much narrower between the lingual end of the protoloph and the anterior margin. The anterior cingulum is absent. The paracone is high and steep-sided, and is connected to the posterior margin of the low round protoconule via a low protoloph. No ectoloph is present. An isolated, ovate mesostyle is present posterior

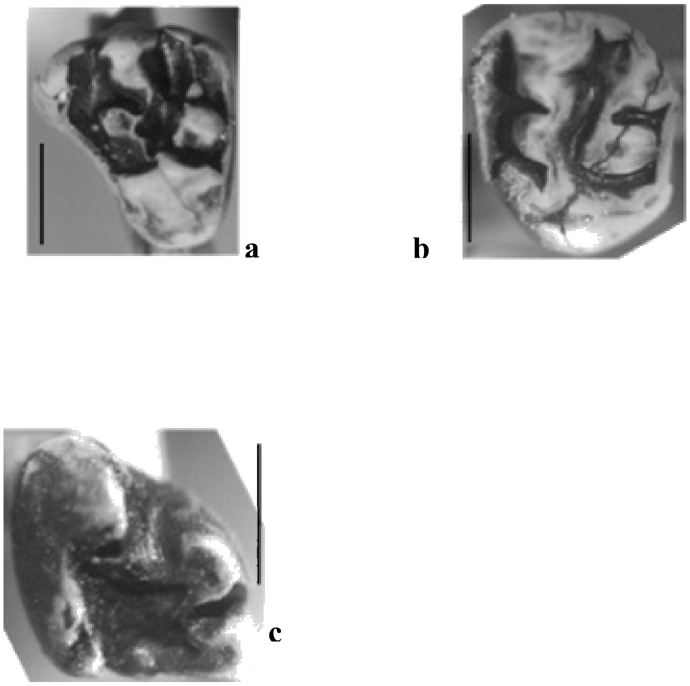


Figure 5.3 *Prosciurus* cf. *P. parvus*: a. SMNH P2521.154 LP4; b. SMNH P2521.321 RM1; c. SMNH P2521.305 Lp4. Scale = 1mm, buccal to top of page.

to the paracone and slightly buccal to the metacone. There are two round metaconules of very different size. The smaller is located buccal to the larger one. The metacone is low and anteroposteriorly compressed. A short, straight metaloph originates from between the mesostyle and the metacone that joins to the small metaconule. The large metaconule expands to contact the posterior margin, but instead of a raised posterior cingulum there is a distinct posterior shelf. No hypocone is clearly present.

The M1 bears a complete protoloph and metaloph that nearly converge buccal to their connection with the protocone. The paracone is joined to the subequally sized protoconule posteriorly by the protoloph. The anterior cingulum is very low, and there is no parastyle at the buccal end. The anterior protocone crest extends from the protocone into the anterior transverse valley on P2521.321 but this is not evident on P2785.021. The mesostyle is small, blocking the relatively narrow central transverse valley. No ectoloph is present. The metacone is connected to the single metaconule anteriorly via the metaloph. The hypocone is present as a small crescentic or ovate fossette at the posterolingual margin, and the posterior cingulum is only clearly present on P2521.321 (not visible on P2785.021, possibly because the posterior margin is very worn).

The trigonid of the p4 is transversely compressed relative to the talonid, and the enamel of the basins is smooth. The metaconid is higher than the protoconid, and both are somewhat cuspate. There is a very narrow anterior cingulid at the anterior base of the protoconid. There is no metalophulid I, but an anteriorly concave metalophulid II borders the posterior margin of the trigonid basin. The ectoloph is low and continuous from the protoconid to the hypoconid. The mesoconid is low, with a buccal mesolophid that continues to the buccal margin. The hypoconid is wide and lower than the protoconid. The posterolophid is high and extends buccally from the entoconid, and is separated from the hypoconid by a narrow gap. No distinct hypoconulid is present. The hypolophid is equal in height to the posterolophid, extending buccally from the anterior margin of the entoconid before curving posterad to join with the hypoconulid. The entoconid is separated by a notch from the mesostylid, which is low and has a slight expansion into the talonid. The mesostylid is joined by a very narrow crest to the metastylid crest, which originates from the posterolingual corner of the metaconid.

Table 5.1 Dental measurements of *Prosciurus* cf. *P. parvus*.

Tooth position	Dimension	N	Mean	OR
P4	AP	1	1.98	
	TR	1	2.18	
M	AP	1	.80	
	TR	1	1.83	
M1	AP	2	1.63	1.45-1.80
	TR	2	2.16	2.08-2.25
p4	AP	1	1.48	
	TRA	1	1.03	
	TRP	1	1.53	

Discussion—*Prosciurus parvus* is the smallest described species of *Prosciurus* (Korth, 1989b). The Rodent Hill specimens are as much as 20% smaller than *P. albiclivus* (Korth, 1994b). The upper teeth are near the upper end of the size range of *P. parvus* given by Korth (1989), whereas the p4 is closer in size to the lower end of the *P. parvus* range. These teeth approximate the size values of *P. relictus* (Korth, 1989b), but the well-developed, buccally expanded mesostyle and the narrow anterior transverse valley of the M1 in the Rodent Hill specimens are more typical of *P. parvus* (wider in *P. relictus*). Also, the metaconule of *P. relictus* is situated further buccad relative to the protoconule than on the Rodent Hill specimens. Furthermore, the P4 of *P. parvus* tends to be smaller relative to M1, as is the case of the Rodent Hill specimens, whereas the P4 is subequal in size to the M1 in *P. relictus* (Korth, 1989b). The only significant difference between the Rodent Hill specimens and the Nebraska *P. parvus* described by Korth (1989) is the doubled protoconules of the Rodent Hill specimens. The relatively large protoconule is a typical feature of *Prosciurus* species except in *P. parvus* (Korth, 1989b), where it is reduced as in other prosciurines (Rensberger and Li, 1986). This is the major reason for considering the Rodent Hill specimens as conferring well with *P. parvus*, but not including them in that species without reservation.

PROSCIURUS SP. INDET. 1

Table 5.2, Figure 5.4a

Referred specimens—SMNH P2521.212 (RM1).

Horizon at Rodent Hill—Collected in stratigraphically uncontrolled sampling.

Description— The M1 has a narrow anterior transverse valley bordered by a low anterior cingulum. The paracone is prominent, while the protoconule is reduced to a narrow widening on the protoloph. The protoloph is complete, higher than the metaloph. The metaloph joins to the protoloph buccal to the protocone. The protocone is very anteroposteriorly compressed, and there is no anterior crest. The paracone bears a slight buccal crest that terminates anterior to the mesostyle. The mesostyle is small and anteroposteriorly compressed, located posterior to the buccal end of the central transverse valley, and with a narrow metastylar crest extended into the central transverse valley. This lophule terminates approximately level with the lingual edge of the metacone. The enamel of the central transverse valley bears some slight rugosity. The metacone is present as a transversely compressed widening on the posterobuccal corner of the tooth that joins to the single, large metaconule by the metaloph. The metaconule is not joined to either the protoloph or the posterior cingulum. A posterior transverse valley is present is present that is about half the width of the anterior transverse valley. The hypocone is a slight swelling of the posterior crest of the protocone, where it has been subsumed into a single loph.

Discussion—P2521.212 is substantially smaller (27% anteroposteriorly; 44% transversely) than any described M1 for *Prosciurus parvus* (Korth, 1989b). It is not included with cf. *P. parvus* described above, as those teeth are appreciably larger. If a distinct species is indicated by this specimen, this would be the smallest *Prosciurus* species, but more material will be necessary. Alternatively, this tooth could be representative of a juvenile specimen.

PROSCIURUS SP. INDET. 2

Table 5.2, Figure 5.4b

Referred specimens—SMNH P2521.399 (RM1 or M2).

Horizon at Rodent Hill—Collected in stratigraphically uncontrolled sampling.

Description—The M1/2 is a very worn tooth that is missing the buccal and anterior margins, and the paracone. The tooth has a protoloph, presumably extending from the paracone, joining to the anterior margin of the protocone apex. The protoconule is large and circular. The mesostyle is present as a slight bump posterior to the location of the paracone blocking the buccal end of the central transverse valley. The enamel of the latter is smooth, and uninterrupted by any lophules. The metacone and metaconule are present as round cusps, with the metaconule smaller. The metaloph extends from the metacone across the front of the metaconule. Buccad to the metaconule is a lingual expansion along the metaloph that is somewhat angular, and could indicate a very worn second metaconule. The metaloph joins the protocone posterior to the site of contact of the protoloph and protocone, although wear appears to exaggerate this feature.

Table 5.2 Dental measurements of *Prosciurus* sp.1 and sp.2.

Taxon	Tooth position	Dimension	N	Mean
Prosciurus sp. 1	M1	AP	1	1.28
		TR	1	1.45
Prosciurus sp. 2	M1-2	AP	1	1.43
		TR	1	2.60

Discussion—The pronounced wear of this specimen makes identification beyond the genus very difficult. It is probably *Prosciurus* due to the simple nature of the occlusal surface, as well as the pronounced protoconule. P2521.399 is at least 15-20% wider (the buccal margin is missing) than the M1 specimens of *Prosciurus* cf. *P. parvus* described above, while it is narrower, probably due to the missing anterior margin of the tooth. The apparent size of this tooth is closer to the range given by Korth (1989b) for

Prosciurus relictus, but the very fragmentary nature of the specimen makes an actual assignment difficult.

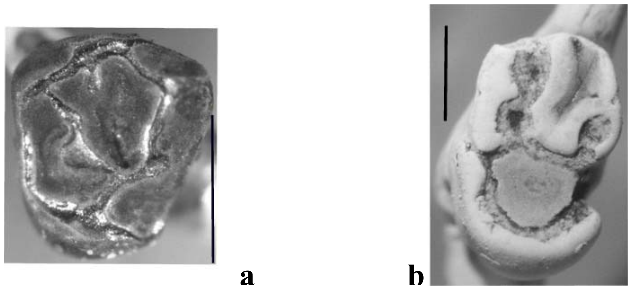


Figure 5.4 *Prosciurus* spp.: a. SMNH P2521.212 RM1; b. SMNH P2521.399 RM1-2. Scale = 1mm, buccal to top of page.

CAMPESTRALLOMYS Korth, 1989b

Type species—*Prosciurus dawsonae* Macdonald, 1963

Referred species—*C. annectens* Korth, 1989b; *C. siouxensis* Korth, 1989b

Age and Distribution—Orellan of Nebraska and Saskatchewan; Whitneyan of Nebraska and Saskatchewan; Arikareean of South Dakota

Diagnosis—"Size near that of *Prosciurus*; dental formula 1-0-1-3; conical anterodorsal expansion of auditory bulla, separated from remainder of bulla by single septum; buccal cusps on upper molars moderately crescentic, dominated by developed ectoloph; mesostyle enlarged and expanded buccally, blocking the central transverse valley of the tooth; protoconules reduced in size compared to those of *Prosciurus* and metaconules single; multiple mesostylids on lower cheek teeth connected to the mesostylid crest; hypolophids very weak or absent on lower molars; i1 flattened anteriorly." Diagnosis given by Korth (1989b).

CAMPESTRALLOMYS SP. INDET.

Table 5.3, Figure 5.5

Referred specimen from Rodent Hill—SMNH P2521.258 (RP4).

Horizon at Rodent Hill—Recovered in stratigraphically uncontrolled sampling.

Description— This P4 has an anterocone that extends strongly forward, with an anterior transverse valley approximately half the width of the central transverse valley. The protoloph is complete and appears to connect to the protocone (which is missing). The crescentic paracone is slightly anteroposteriorly compressed and larger than the protoconule, to which it is joined posteriorly by the protoloph. The paracone and metacone are distinct, crescentic-shaped cusps. The ectoloph is not present between the mesostyle. The mesostyle is distinct, originating along the buccal margin, buccally to the paracone and metacone. A well-developed metastylar crest extends lingually from the mesostyle into the central transverse valley and terminates about level with the centre of the paracone. Otherwise, there are no accessory lophules or crests in the central transverse valley, and the enamel is smooth. The metacone is subequal in size to the paracone. The metaloph extends from the lingual margin of the metacone and

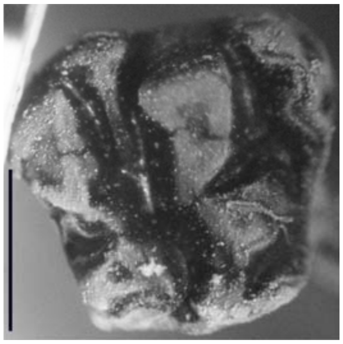


Figure 5.5 *Campestrallomys* sp indet.: SMNH P2521.258 RP4. Scale = 1mm, buccal to top of page.

terminates as a small extension past the metaconule. The metaconule does extend to the posterior margin, where there is no obvious posterior cingulum, but there is a pronounced posterior labial fossette between the metacone and metaconule. Both conules are well developed, but smaller than the main cusps.

Discussion—The well-developed mesostyle and mesostylar crest, crescentic cusps and estimated size of this P4 indicate that it is very similar to the genus *Campestrallomys*. The dominance of the buccal cusps over the ectoloph is especially reminiscent of the *C. siouxensis* upper molars described by Korth (1989b); however, the incomplete ectoloph is more reminiscent of *C. annectens* (Korth, 1989b). In the latter species the ectoloph is best developed between the paracone and mesostyle, which is not seen in the Rodent Hill specimen. Unfortunately, it is the only specimen that appears referable to the genus, and it is broken, so the actual size is unknown. Anteroposteriorly, P2521.258 is roughly 13% shorter than *C. siouxensis*, but it is about 10% larger than *C. annectens*. It seems more appropriate at this time to refer the Rodent Hill specimen to *Campestrallomys* sp. indet., but not assign it further until more fossil material becomes available.

Table 5.3 Dental measurements of *Campestrallomys* sp. indet.

Tooth position	Dimension	N	Mean
P4	AP	1	2.00
	TR	1	1.80

HAPLOMYS Miller and Gidley 1918

Type species—*Meniscomys liolophus* Cope, 1881

Referred species—*H. arboraptus* (Shevyreva, 1971); *H. galbreathi* Tedrow and Korth, 1997.

Age and Distribution—Orellan of South Dakota and Saskatchewan; Whitneyan of Oregon and Saskatchewan; middle Oligocene of Mongolia and Kazakhstan.

Diagnosis—"Small to intermediate sized prosciurines (equal or larger than *Prosciurus*); cheek teeth brachydont as is typical of prosciurines; fourth premolars equal in size to first molars (uppers and lowers) instead of enlarged as in other aplodontid subfamilies; lower cheek teeth rhomboidal as in *Prosciurus* but more lophate; less lophate than lower cheek teeth of meniscomyines; variable presence on later species of typical Allomyinae fossettid formed by anterobuccal extension of the hypoconid and buccal mesolophid, while earlier species show beginnings of an anterior extension on the hypoconid; upper cheek teeth bear more prominent parastyle and mesostyle than in *Prosciurus*; weak ectoloph on upper cheek teeth that is absent in other prosciurines but well developed in all other aplodontids; single metaconule instead of doubled as in Allomyinae". From Tedrow and Korth (1997).

HAPLOMYS CF. *H. LIOLOPHUS* (Cope, 1881)

Table 5.4, Figure 5.6 a-c

Meniscomys liolophus Cope, 1881; 1883

Holotype—AMNH 6987 (Left maxillary, P4-M2), John Day Formation, Oregon (Whitneyan).

Referred specimens—SMNH P2836.004 (Rp4); P2836.008 (Lm2); P2452.128 (Lm3).

Horizon at Rodent Hill—Specimens P2836.004 and P2836.008 recovered from Stratigraphic Unit V; P2452.128 recovered in stratigraphically uncontrolled sampling.

Emended diagnosis—Largest species of genus; ectoloph distinct and often interrupted at central transverse valley unlike *H. arboraptus*; paracone of P4 larger than protoconule; protoconule of M1-M3 subequal in size to paracone (paracone larger than protoconule in *H. arboraptus*); protoloph and metaloph of M1-M3 not straight but sharply angled, slightly curved or straight on P4 (only slightly curved in *H. arboraptus*). Lower teeth more lophate than *H. galbreathi*; anterior extension of hypoconid pronounced, may join to metastylid crest to form a posterior buccal fossettid (extension weak in *H. galbreathi)*; mesostylids extended transversely (absent in *H. arboraptus*). A diagnosis was originally given by Cope (1883), based entirely on uppers. This emendment seeks to clarify the Cope (1883) diagnosis and include the lower dentition described by Rensberger (1975).

Description—The metaconid and protoconid of the p4 are close together, giving the tooth a compressed trigonid relative to the talonid. The protoconid and metaconid are relatively high and cuspate. Metalophulid I is very low and extends anterad from the protoconid and metaconid and is convex anteriorly. Metalophulid II extends posterad from the buccal margin of the metaconid, is faintly joined to the protoconid, and is concave into the basin, widening the trigonid. The trigonid and talonid basins both have smooth enamel. The ectolophid is low, just above the basin, and runs straight from the protoconid to the mesoconid, with a slight buccal curve from the mesoconid to the hypoconid. The mesoconid is well developed and lower than the other buccal cusps, with a distinct mesolophid that extends to the buccal margin. The anterior crest of the hypoconid extends toward and connects weakly with the buccal end of the mesolophid. This gives the posterior buccal fossettid a slightly sloped appearance. The hypoconid is high, cuspate, and is transversely widened and buccally expanded, adding to the width of the posterior of the tooth. The posterolophid extends from the lingual edge of the hypoconid, across the posterior of the hypoconulid to the buccal margin of the entoconid. The hypoconulid is cuspate, anteroposteriorly compressed, and raised above the posterolophid. A low crest extends from the hypoconulid to the posterolingual corner of the mesoconid. The entoconid is the lowest of the four major cusps (possibly a wear feature) and is separated from the mesostylid by a deep notch. The metaconid bears a tiny cuspule on the posterolingual margin, from which the mesostylid ridge extends. The mesostylid ridge terminates in a very low, transversely compressed mesostylid.

Table 5.4 Dental measurements of *Haplomys* cf. *H. liolophus*.

Tooth position	Dimension	N	Mean
p4	AP	1	2.33
	TRA	1	1.40
	TRP	1	2.30
m2	AP	1	2.05
	TRA	1	1.63
	TRP	1	1.30
m3	AP	1	2.90
	TRA	1	inc
	TRP	1	inc

P2836.008 is the buccal half of an m2. The protoconid is high and cuspate, with a metalophulid II extending from the posterolingual across the trigonid. The ectolophid is low, concave buccally between the protoconid and mesoconid, and again between the mesoconid and hypolophid. The mesoconid is well developed, slightly higher than the ectolophid, with a heavy mesolophid extending to the buccal margin. The anterior crest of the hypoconid extends toward the buccal mesolophid, but does not join with it. The hypoconid is cuspate, but lower and smaller than the protoconid. The hypoconid bears a narrow posterobuccal cingulum as well as the well-developed posterolophid extending from its lingual margin. The posterolophid extends to the very anteroposteriorly

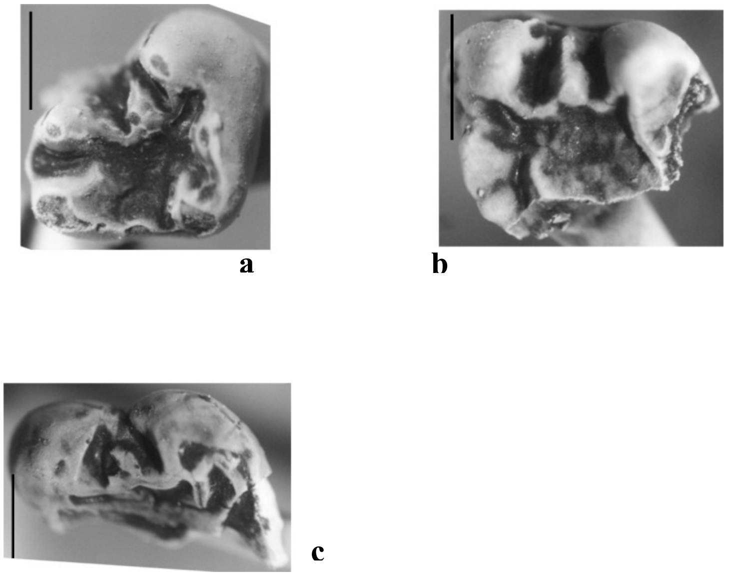


Figure 5.6 *Haplomys* cf. *H. liolophus:* a. SMNH P2836.004 Rp4; b. SMNH P2836.008 Lm2; c. SMNH P2452.128 Lm3. Scale = 1mm, buccal to top of page.

compressed hypoconulid. The lingual portion of the hypolophid terminates anterior to the hypoconulid, approximately midway across the talonid basin, but the origin of this loph is unknown. The enamel of the trigonid and talonid basins bears no distinct pits, lophules or crenulations but do appear slightly wrinkled.

P2452.128 is the buccal half of a m3. The enamel of the trigonid and talonid basins appears smooth, although little enamel is present. The cuspate protoconid is large and high, with a very short crest extending into the trigonid basin. Metalophulid I extends from the anterior of the protoconid and curves linguad to extend across the anterior of the tooth. The ectolophid is low, and extends straight from the protoconid to the anterior margin of the hypoconid. The mesoconid is well developed and large, with a strong buccal mesolophid that is separated from the anterior crest of the hypoconid by a notch, creating a nearly enclosed posterior buccal fossettid. A posterior buccal crest extends posterad from the protoconid and nearly joins with the buccal end of the mesolophid. The hypoconid is slightly smaller than the protoconid, and is equally cuspate. The union with a hypolophid is not apparent due to breakage, but there is the indication that the posterolophid does join to the lingual margin of the hypoconid.

Discussion—The material described here is very similar to previously described specimens for this taxon, in both morphology and size. The lowers are almost identical to those described by Rensberger (1975).

DAKOTALLOMYS TEDROW and Korth, 1999

Type species—*Dakotamys pelycomyoides* Tedrow and Korth, 1997

Referred species— *Dakotallomys lillegraveni* (Tedrow and Korth, 1997)

Age and distribution—Orellan and Whitneyan of South Dakota; and Whitneyan of Saskatchewan.

Diagnosis—"Medium to large sized prosciurines, larger than *Prosciurus*, equal to or smaller than *Pelycomys*; mesostylid on lower cheek teeth small and attached to metastylid crest as in some species of *Pelycomys;* differs from all other prosciurines in the presence of a unique labial cingulum of protoconid and hypoconid of lower cheek teeth; hypolophid complete on m1-m2 as in *Pelycomys*; lower incisor wider in relative length than *Pelycomys* and other prosciurines". Originally given by Tedrow and Korth (1997). Presence of weak ectoloph in P4 and M3 that is not found in *Pelycomys*.

Discussion—The diagnosis for the genus *Dakotallomys* is emended here to include diagnostic information about the upper teeth, as Tedrow and Korth (1997) did not describe them.

DAKOTALLOMYS CF. *D. PELYCOMYOIDES* Tedrow and Korth, 1997

Table 5.5, Figure 5.7 a-c

Type specimen—UCMP 82834, right mandible with p4-m3, Backward Butte, Harding County, South Dakota (Whitneyan).

Referred specimens—SMNH P2794.037 (LP4); P2834.001 (RM3); P2834.003 (LM3); P2454.042 and P2521.084 (Rm2).

Horizon at Rodent Hill—P2834.001 and P2834.003 collected from Stratigraphic Unit I; all others collected in stratigraphically uncontrolled sampling.

Diagnosis—Differs from *D. lillegraveni* in being 20% larger. Lowers with more robust cusps and relatively larger entoconids and mesostylids on the lower molars, and lacking buccal mesolophids. From Tedrow and Korth (1997).

Description—The P4 has a large, anteriorly expanded anterocone and a narrow anterior cingulum. The protoloph is complete and joins the apex of the protocone. The protoloph connects to the anterior margin of the anteroposteriorly compressed paracone and the subequal, ovate protoconule. No anterior protocone crest extends into the anterior transverse valley. The paracone is set well in from the buccal margin, and the buccal face of the paracone has two anteroposteriorly-compressed fossettes. These fossettes are produced by the very narrow, very poorly developed ectoloph originating from the parastyle. The ectoloph continues along the buccal margin, through the mesostyle, and terminates at the metacone. The mesostyle is anteroposteriorly elongate, buccally expanded, and is the origin of a mesoloph that runs lingually into the central transverse valley, which is otherwise smooth and without accessory lophules or crests. The metaloph is complete and subparallel to the protoloph, but does not join to the protoloph or protocone. The metacone is anteroposteriorly elongate, set further linguad than the paracone, with a wider fossette present at its anterobuccal corner. The metacone is joined anteriorly to a smaller metaconule by the metaloph. The small metaconule then joins to the anterior margin of a much larger metaconule via the metaloph. This larger metaconule is ovate and extends to the posterior margin of the tooth, where no posterior cingulum or hypocone is present, but a posterior buccal fossette is well developed.

M3 has a wide anterior transverse valley and an anterior cingulum that may be level with or higher than the parastyle. The protoloph is complete, much higher than the anterior cingulum or metaloph, and originates from the center of the anteroposteriorly-compressed paracone. A very tiny protoconule is present on P2834.003, but not on

P2834.001. The protoloph connects with, or near, the apex of the protocone. The anterior protocone crest is wide and extends well into the center of the anterior transverse valley. There is a weak buccal fossette on the paracone, as well as a weak posteriorly directed crest that terminates at the anterior margin of the central transverse valley. The mesostyle is present only on P2834.003 as a very tiny, isolated cuspule with a very short metastylar crest extended lingually into the central transverse valley. The metacone is very low and broad posterior to the metaloph. The metaloph is complete, originating from the buccal margin very close to the mesostyle, and anterior to the metacone. The metaloph connects with the anterior margin of the large, single metaconule. On P2834.001, the metaloph terminates here, whereas on P2834.003 the metaloph extends to the protocone, posterior to the site of union of the protoloph. The metaconule is anteroposteriorly elongate, extends to the protoloph on P2834.001, and extends to the posterior cingulum on both specimens. The posterobuccal corner of both teeth is expanded posteriorly, but more so on P2834.001, giving the M3 a triangular outline. This expansion is rimmed by a low posterior cingulum. The hypocone, which

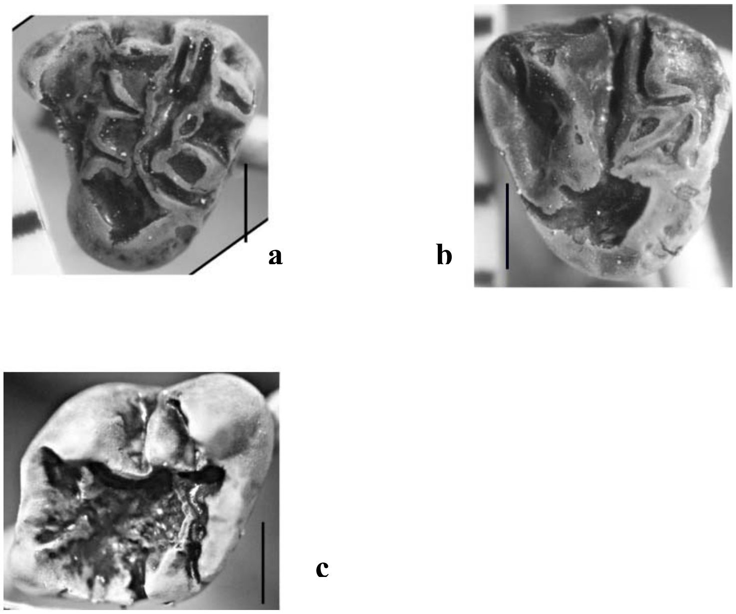


Figure 5.7 *Dakotallomys* cf. *D. pelycomyoides*: a. SMNH P2794.037 RP4; b. SMNH P2834.003 LM3; c. SMNH P2521.084 Rm2. Scale = 1mm, buccal to top of page.

is reduced and anteroposteriorly compressed, is present as the lingual terminus of the posterior cingulum.

The protoconid and metaconid of m2 are of equal height and size. The metaconid may be situated slightly anterad of the protoconid. On P2521.084, which is much less worn, the metalophulid II is much lower than the anterolophid and is poorly developed at the metaconid. On the protoconid end of metalophulid II two tiny cuspules are present. The trigonid is small, about 1/3rd the length of the talonid, and is also slightly narrower. Only the talonid basin of P2521.084 bears any rugosity as a slight wrinkling of the enamel. The ectolophid is well developed, lower than the anterolophid, and extends posterobuccally to the junction of the hypoconid and the posterolophid. The mesoconid is also well developed, is higher than the ectolophid, and is linguad to a buccal shelf that separates the protoconid and hypoconid. No buccal mesolophid is present, but the mesoconid of P2521.084 has a slightly expanded base that does not join with the anterior hypoconid crest. The hypoconid is large with some buccal expansion. A narrow buccal cingulum is present buccad to the hypoconid of P2521.084 that is not apparent on the protoconid; the buccal enamel of P2452.042 is broken away. The posterolophid joins to the lingual edge of the hypoconid, and continues lingually to terminate at the entoconid, or just buccal to it. The hypoconulid is present as an anterior swelling at the center of the posterolophid. The hypolophid extends buccally from the entoconid to either join the ectolophid or terminate in the middle of the talonid basin, anterior to the hypoconulid. A small, anteriorly directed lophule extends from the entoconid into the talonid basin, and terminates approximately level with the mesostylid. The entoconid is separated from the mesostylid by a deep notch. On the less worn P2521.084, the mesostylid is well developed, although lower than all other cusps and cuspules on the tooth, and its base swells slightly buccally into the talonid basin. The mesostylid crest originates from the posterior margin of the metaconid, and terminates by connecting to the mesostylid.

Discussion—These specimens are the first record of *Dakotallomys* outside of South Dakota, and extend the known range further north into southern Saskatchewan. The lower molars that are referred to this species are no more than 10% smaller than the South Dakota specimens. The narrow buccal cingulum on the protoconid of m2

(P2521.084) is what clearly distinguishes this specimen as *Dakotallomys*, as opposed to the very similar *Pelycomys*. The P4 and M3s listed above are the first upper teeth referred to the genus; referral is based primarily on their similar size to the lowers. These teeth are the largest upper aplodontid teeth recovered from the Rodent Hill Locality, so without another similarly sized option in the rodent fauna it is reasonable to associate them with the lowers. The morphology of the upper cheek teeth is very similar to that of *Pelycomys*, as noted by Tedrow and Korth (1997) in their initial description of the lower cheek teeth of *Dakotallomys*. The generic diagnosis has been emended, but the species diagnosis cannot be properly emended until uppers of the congeneric *D. lillegraveni* are identified and described. For now, the specific diagnosis of the upper teeth is as for the genus until the uppers of *D. lillegraveni* are described.

Table 5.5 Dental measurements of *Dakotallomys* cf. *D. pelycomyoides*.

Tooth position	Dimension	N	Mean	OR
P4	AP	1	3.00	
	TR	1	3.15	
M3	AP	2	2.90	2.90-2.90
	TR	2	3.18	3.10-3.25
m2	AP	2	2.95	2.80-3.10
	TRA	2	2.60	2.60-2.60
	TRP	2	2.75	2.70-2.80

ALLOMYINAE Marsh, 1877

PSEUDALLOMYS Korth, 1992a

Type Species—*Pseudallomys nexodens* Korth, 1992a

Referred Species—*P. korthi, sp. nov.;* Fossil Bush *Pseudallomys, sp. nov.,* Meyer, 2003

Age and distribution—Orellan of Saskatchewan and Montana, Whitneyan of Saskatchewan.

Emended Diagnosis—Intermediate-sized aplodontid; complex network of lophules in the basins of the upper and lower cheek teeth. Uppers with complete ectoloph; mesostyle buccally prominent, protoloph and metaloph complete, converge buccal to protocone, anterior cingulum usually joined to protoloph via narrow crest; small but not minute metaconule variably present, hypocone well-developed. Lowers with variably present anterior cingulid anterad to protoconid, anteroposteriorly compressed metaconid, complete hypolophid, broad shelf at base of crown buccal to large mesoconid, doubled mesostylid on at least M_2-$M_{3,}$ long buccally running lophule from both mesostylids, large hypoconulid. Lowers originally diagnosed by Korth (1992), Meyer (2003) diagnosed the uppers. This emendment seeks to combine their diagnoses and include information from the Rodent Hill species.

Discussion—Korth (1992a) described the genotypic material of *Pseudallomys* based on a single lower tooth row. Meyer (2003) described a new species of *Pseudallomys* from the Orellan Fossil Bush Locality that included both lowers and uppers. No name was given to the Fossil Bush species, and it will be referred to herein as Fossil Bush *Pseudallomys*.

PSEUDALLOMYS KORTHI SP. NOV.

Table 5.6, Figure 5.8 a-f

Holotype—SMNH P2521.309 (Lm3), Rodent Hill Locality.

Referred specimens—SMNH P2521.314 (RP4); P2521.160 and P2521.185 (LP4); P2521.157 (LM1); P2834.008 (RM1); P2521.250 and P2835.006 (LM2); P2834.010; (Lp4); P2521.049 (Rp4); P2452.131 and P2834.017 (Lm1 or m2); P2521.085 (Lm2); P2521.309 (Lm3).

Etymology—Patronym for William W. Korth for his many contributions to the study of Tertiary rodents.

Horizon at Rodent Hill—P2834.008, P2834.010 and P2834.017 from Stratigraphic Unit I, P2835.006 from Unit II. All other specimens in stratigraphically uncontrolled sampling.

Diagnosis—About 25% smaller than *P. nexodens*; similar in size to Fossil Bush *Pseudallomys*. P4 less anteroposteriorly elongate than in Fossil Bush *Pseudallomys*; M1-2 about 30% wider than Fossil Bush *Pseudallomys*; upper molars with well-developed ovate hypocone (round in Fossil Bush *Pseudallomys*); lowers have doubled mesostylids (Fossil Bush *Pseudallomys* has a single mesostylid); m2 anteroposteriorly more elongate than in *P. nexodens*; trigonid not transversely compressed as seen in *P. nexodens* or Fossil Bush *Pseudallomys*; m3 more anteroposteriorly compressed than *P. nexodens*; lophules of trigonid and talonid basins less complex than in Fossil Bush *Pseudallomys*, similar to those of *P. nexodens*.

Description—All of the cheek teeth of this taxon bear a number of small lophules in the central transverse valleys of the uppers and in the talonid basins of the lowers.

The anterocone of the P4 is anteroposteriorly compressed, extending lingually about midway down the anterior transverse valley. A complete protoloph connects the paracone and subequally sized protoconule along their posterior margins. The ectoloph is complete, forming steep buccal fossettes buccad to the anterior of the paracone,

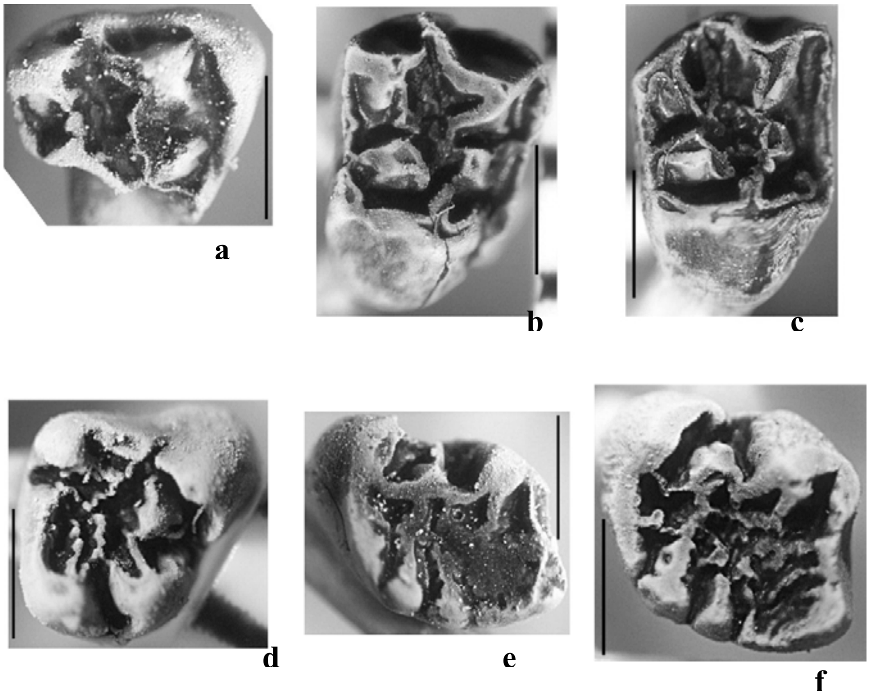


Figure 5.8 *Pseudallomys korthi*: a. SMNH P2521.314 LP4; b. SMNH P2834.008 RM1; c. SMNH P2835.006 LM2; d. SMNH P2834.010 Lp4; e. SMNH P2521.085 Lm2; f. SMNH P2521.309 Lm3. Scale = 1mm, buccal to top of page.

between the paracone and mesostyle, and between the mesostyle and metacone. The mesostyle is very small, nearly subsumed into the ectoloph, and situated buccally relative to the paracone and metacone. A very short metastylar crest extends into the central transverse valley of P2521.185. The metaloph extends from the metacone lingually to a tiny expansion that may be a small second metaconule. The metaloph extends beyond this point to the larger metaconule. The large metaconule contacts the narrow posterior cingulum by a low crest, and approaches the protoloph by another low crest. The posterior buccal fossette and posterior lingual inflection are both closed to the posterior of the tooth by the posterior cingulum. No hypocone is present.

On the less worn M1 specimens, the metaloph and protoloph are complete, uniting buccal to the protocone before joining to the protocone by a narrow crest. The protoloph is straight, joining the paracone and slightly smaller protoconule along their posterior margins. The protoloph is connected to the anterior cingulum by a low crest that extends from the buccal margin of the protoconule. The anterior protocone crest extends well into the anterior transverse valley. There is a well-developed ectoloph along the buccal edge of the tooth, producing three steep fossettes. The mesostyle is poorly developed and expanded buccally, and has a lingually directed metastylar crest extending into the central transverse valley. This metastylar crest joins to the smaller, more buccal, of the two metaconules that forms a steep sided fossette anterior to the metacone of P2834.008. The metacone is small, and joins to the anterior of the small metaconule via the metaloph. The metaloph then connects with the larger, transversely compressed lingual metaconule before continuing to join with the protoloph. The larger metaconule connects with the protoloph and the posterior cingulum via low crests. The posterior cingulum of P2834.008 bears a tiny cuspule situated approximately halfway between the metacone and larger metaconule. A small, but distinct, ovate hypocone is present at the union of lingual terminus of the posterior cingulum and the posterior protocone crest.

The M2 is morphologically similar to the M1, except that the protoloph is not straight but instead is wavy, and there are more small lophules extending into the anterior transverse valley from the protoloph.

The p4 has a tiny anteroconid at the center of an interrupted metalophulid I, and the somewhat anteroposteriorly compressed metaconid and protoconid are separated by a deep valley. The metalophulid II is an anteriorly concave ridge extending from the posterior margins of the anterior cusps. From this ridge, a posteriorly directed crest extends to the center of the tooth. The ectolophid is well developed, and terminates anterior to the hypoconid. The mesoconid is present, buccad of which is a broad shelf between the protoconid and hypoconid. There is also a buccal mesolophid extending almost to the buccal margin that nearly joins the anterior hypoconid crest, but does not quite enclose the posterior labial fossettid. The hypoconid is expanded posterobuccally, and is separated from the posterolophid by a deep notch. The hypoconulid is present as an anteroposteriorly-compressed expansion of the posterolophid, and is the origin of a crest that extends anteriorly to the center of the tooth. The posterolophid terminates just before reaching the entoconid. A hypolophid extends buccad from the entoconid, but is interrupted by the crest that extends from the hypoconulid. The entoconid is separated by a wide gap from the metastylar ridge, which originates from the metaconid. There are no definite mesostylids, but the posterior end of the metastylar ridge bears some small, widened areas. . In P2834.010 (the better preserved p4) a small crest extends from the metastylid ridge that extends transversely across the tooth to interrupt the hypoconulid lophule and the metalophulid II lophule. A second, posteriorly directed low crest originates at the posterior margin of the metaconid and curves slightly linguad before terminating beside the metastylid crest.

Both m1/m2 specimens are broken, making precise identification uncertain. The m1/m2 have an incomplete metalophulid I; it is also separated by a notch from the protoconid. The ectolophid is strong, and reaches the large, crescentic hypoconid. A large mesoconid with a well-developed buccal mesoloph extends along the deep buccal shelf. On P2834.017, the wear is sufficient that the buccal mesolophid has joined with the anterior hypoconid crest to enclose the posterior labial fossettid. The posterolophid is narrow and extends across the posterior margin of the tooth. The hypoconulid is anteroposteriorly compressed, and the entoconid is large and separated by notches from the metastylid ridge and from the posterolophid. The hypolophid is complete. On P2452.131 there are two visible metastylids along the metastylid ridge, the more posterior one has a transverse lophule that extends across the width of the tooth.

The m2 (P2521.085) is fairly worn, with only the largest basin lophules still visible and the buccal edge of the hypoconid broken off. It has a complete metalophulid I between the protoconid and metaconid, and an incomplete metalophulid II extending buccally from the protoconid that terminates midway across the trigonid. A short process present on the anterior margin of the protoconid may be an anterior cingulum. The metalophulid II encloses a small basin fossettid by joining with the ectolophid and a small lophule extended from the ectolophid. The ectolophid extends to the hypoconid. The mesoconid is large with a deep buccal shelf and a buccal mesolophid extended to the buccal margin. The portion of the hypoconid that is present is large and crescentic. The posterolophid extends from the lingual edge of the hypoconid across the hypoconulid and terminates before reaching the entoconid, which is also separated by a gap from the metastylid ridge. A low crest extends anterad from the hypoconulid, and a

Table 5.6 Dental measurements of *Pseudallomys korthi*. Holotype SMNH 2521.309 (Lm3)

Tooth position	Dimension	N	Mean	OR	Holotype
P4	AP	2	1.75	1.68-1.83	
	TR	1	2.23		
M1	AP	3	1.60	1.53-1.70	
	TR	3	2.34	2.25-2.50	
M2	AP	2	1.59	1.53-1.65	
	TR	2	2.09	1.90-2.28	
p4	AP	1	1.75		
	TRA	2	1.36	1.33-1.40	
	TRP	1	1.80		
m1-2	AP	2	1.76	1.73-1.80	
	TRA	2	1.38	1.33-1.43	
	TRP	2	1.55	1.53-1.58	
m2	AP	1	1.83		
	TRA	1	1.53		
	TRP	1	1.63		
m3	AP	1	1.93		1.93
	TRA	1	1.65		1.65
	TRP	1	1.63		1.63

second, parallel crest extends from the posterolophid, just lingual to the hypoconulid. The hypolophid is complete, extending from the entoconid to the ectolophid. The metastylid ridge extends posteriorly from the metaconid, and joins with two mesostylids that both have buccally oriented lophules that extend into the talonid basin.

The m3 has a complete metalophulid I that bears several posteriorly directed crests that extend across the trigonid basin. The incomplete metalophulid II extends linguad from the protoconid. The protoconid has a flattened surface. The ectolophid is well developed and continuous to the hypoconid. The mesoconid is large with a wide buccal shelf but no discernable buccal mesolophid. The hypoconid is large and expanded posteriorly, and the anterior hypoconid crest extends to midway across the metastylar shelf. The posterolophid extends from the lingual margin of the hypoconid, across the distinct hypoconulid, and then terminates before contacting the entoconid. The entoconid is large and separated from the metastylid ridge. The hypolophid is complete, extending from the entoconid to the ectolophid. A small anteroposteriorly directed lophule connects the hypoconulid and the hypolophid. The mesostylids are doubled, and continuous with the mesostylid ridge that originates at the anteroposteriorly-compressed metaconid. Each mesostylid has a crest extending from it transversely into the basin.

Discussion—The few specimens (P2521.085 (Lm2) and P2521.309 (Lm3)) of this taxon that are comparable with the genotype from Montana (CM 11898), are both smaller than the teeth of *Pseudallomys nexodens*, and the proportions are quite variable (5 and 26% smaller anteroposteriorly for the m2 and m3, respectively; and 22 and 15% smaller transversely). The upper teeth are referred to *Pseudallomys* based upon their similarity to the species described by Meyer (2003) from the Orellan-age Fossil Bush Locality. The lophulate enamel of the basins of the cheek teeth and the doubled mesostylids on the Rodent Hill specimens are particularly indicative of the genus *Pseudallomys*. The substantial difference in size and proportions from *P. nexodens* distinguish *P.* sp. 1 from that species; the distinct differences in the crenulations and the more robust stylid cusps of the Fossil Bush *Pseudallomys* indicate that the Rodent Hill material represents a separate species.

PARALLOMYS Rensberger1983

Type species—*Plesispermophilus ernii* Stehlin and Schaub, 1951

Referred species—*P. argoviensis* (Stehlin and Schaub, 1951); *P. macrodon* (Schmidt-Kittler and Vianey-Liaud, 1979); *P. americanus* Korth, 1992.

Age and distribution—Late Oligocene of France, Switzerland, and Germany; Whitneyan of Saskatchewan; Arikareean of Nebraska and Saskatchewan.

Diagnosis—"Upper cheek teeth with broad, U-shaped central transverse valley, low protoloph, metaloph. Central, anterior, posterior transverse valleys without accessory crests; walls smooth to faintly crenulated. Labial faces of paracone, metacone sloping strongly linguad; metastylar crest trending strongly labiad. Lower cheek teeth basined, internal crests low or absent, never reaching center of diagonal valley. Posterointernal crest of mesoconid (ectolophid) not connected to hypoconid". Given by Rensberger (1983).

PARALLOMYS SP.

Table 5.7, Figure 5.9

Referred specimen from Rodent Hill—SMNH P2838.001 (LP4).

Horizon at Rodent Hill—Stratigraphic Unit VII.

Description—This P4 has a well-developed, anteriorly expanded anterocone with a lingual anterostyle. There is a broad anterior transverse valley. The protoloph is complete and high, originating from the posterior corner of the paracone. The paracone is large and steep-sided, and connects to the posterior margin of the smaller round protoconule via the protoloph. The protoloph connects to the protocone anterior to its apex. The anterior protocone crest extends well into the anterior transverse valley. The lingual margin of the tooth bears a narrow cingulum. The ectoloph is complete and very well developed, originating at the parastyle and terminating at the posterior margin of the tooth. The parastyle and mesostyle are not distinct; instead they are subsumed into the ectoloph. The metastylar crest extends buccally from the ectoloph to the buccal margin of the tooth. The ectoloph has two large buccal fossettes, anterior and buccad to the paracone and metacone. There is a low buccal cingulum situated below each buccal fossette. The metacone is also steep-sloped, but smaller and more crescentic than the paracone. The metaloph extends from the lingual apex of the metacone, connecting to two metaconules. The buccal-most metaconule is slightly smaller and somewhat crescentic in shape. The second, lingual metaconule is round in shape and is located slightly more anterior relative to the first metaconule. The posterior labial fossette is pronounced, and posterior extensions from both metaconules create a second posterior fossette. The metaloph terminates at the lingual metaconule, leaving the posterior lingual inflection open to the central transverse valley. The hypocone is present as a sliver-shaped, anteroposteriorly-compressed cusp at the lingual terminus of the posterior margin. The posterior margin is barely raised above the level of the posterior transverse valley, and so cannot properly be called a posterior cingulum. The central transverse valley is relatively wide and free of accessory crests except for a very small crest that extends posteriorly from the lingual edge of the paracone. A larger lophule extends anterad from the anterior face of the lingual metaconule and terminates in the center of the valley as a circular cuspule.

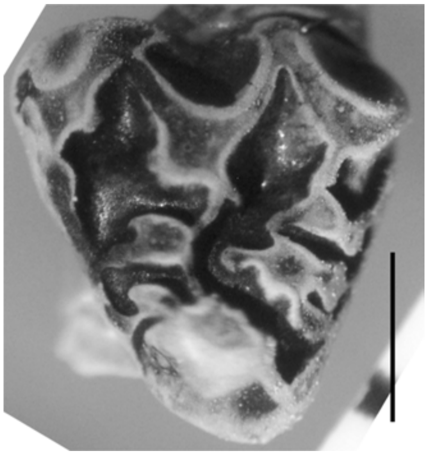


Figure 5.9 *Parallomys* sp: SMNH P2838.001 LP4. Scale = 1mm, buccal to top of page.

Discussion— To date, only one specimen of this aplodontid has been recovered from the site, so any specific assignment will require more material. This specimen is smaller than any of the other species of *Parallomys*, being almost 60% shorter anteroposteriorly than the P4 of *P. americanus* described by Storer (2002), and about 35% shorter than any upper tooth of *P. americanus* described by Korth (1992) or Storer (2002). Furthermore, *P. americanus* is itself relatively small compared to the European species (Rensberger, 1983).

Table 5.7 Dental measurements of *Parallomys* sp.

Tooth position	Dimension	N	Mean
P4	AP	1	2.30
	TR	1	2.68

6. FAMILY SCIURIDAE

The Sciuridae includes modern squirrels, marmots, chipmunks and flying squirrels, a very diverse group that is found on every continent except Australia and Antarctica (Mercer and Roth, 2003; de Bruin, 1999; Korth, 1994a). Sciurids probably originated from an ischromyid ancestor (Korth, 1994a). The earliest known sciurid, *Douglassciurus jeffersoni* has been found from the middle Chadronian of North America (Mercer and Roth, 2003; Emry and Korth, 1996; 2001), and the family quickly radiated throughout the Northern hemisphere by the early Oligocene (Mercer and Roth, 2003; de Bruijn, 1999). The sciurids entered Africa in the middle Miocene, and appeared in South America after the closing of the Panama land bridge (Mercer and Roth, 2003).

The jaw angle of all known sciurids is sciurognathous, and most sciurids have a sciuromorphous zygomasseteric structure (Korth, 1994a). The exceptions to this are the earliest sciurid *Douglassciurus jeffersoni*, which has a protrogomorphous zygomasseter (Korth, 1994a) and the cedromurine sciurids that may demonstrate a modified myomorphic zygomasseter (Korth, 1994a; Korth and Emry, 1991).

The dental formula of most sciurids is 1023/1013 except for the North American genus *Tamias* and a few African genera, where the P3 is lost (Korth, 1994a). Sciurid upper dentition (**Figure 6.1**) can be recognized by having three main cusps (paracone, metacone and protocone) and weak or absent conules, except in some pteromyines (de Bruin, 1999). The lower dentitions of sciurids (**Figure 6.2**) have four main cusps (protoconid, metaconid, hypoconid and entoconid), but the entoconid is sometimes poorly developed or subsumed within the protolophid (de Bruin, 1999).

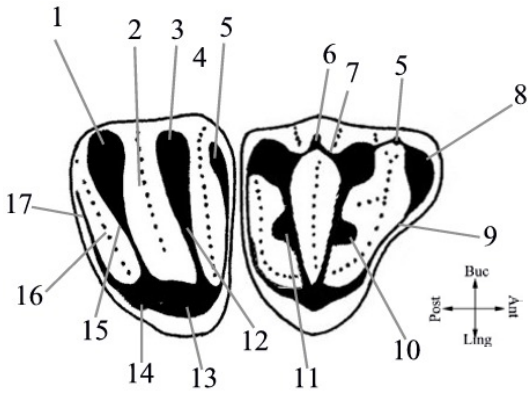


Figure 6.1 Generalized sciurid upper cheek tooth morphology. RM1-2 (on left) and RP4 with major features identified. 1–metacone 2—central transverse valley 3—paracone 4—anterior transverse valley 5—parastyle 6—mesostyle 7—ectoloph 8—anterocone 9—anterior cingulum 10—protoconule 11—metaconule 12—protoloph 13—protocone 14—hypocone 15—metaloph 16—posterior transverse valley 17—posterior cingulum

Drawn by Taran Meyer, modified by the author. Terminology from Wood and Wilson (1936) and Black (1963)

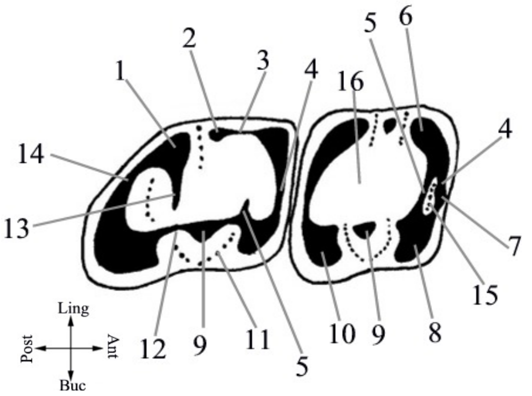


Figure 6.2 Generalized sciurid lower cheek tooth morphology. Rm1-2 (on right) and Rm3, with major features identified. 1—entoconid 2—mesostylid 3—metastylid crest 4—metalophulid I (=anterior cingulum) 5—metalophulid II 6—metaconid 7—anteroconid 8—protoconid 9—mesoconid 10—hypoconid 11—metastylar shelf 12—ectolophid 13—hypolophid 14—posterolophid (=posterior cingulum) 15—talonid 16—trigonid

Drawn by Taran Meyer, modified by the author. Terminology from Wood and Wilson (1936) and Black (1963)

Variations in the dentition make the three main groups of sciurid recognizable. In ground squirrels (Marmotini, Tamiini), the lophs of the upper teeth converge at the protocone, the metaloph of P4-M2 is incomplete, the entoconid is submerged within the posterolophid (de Bruin, 1999) and the teeth are lophate with less distinct cusps (Korth, 1994a). Tree squirrels (Sciurini) are distinguished by a complete metaloph on P4-M2, subparallel upper lophs, a distinct entoconid (de Bruin, 1999) and low, rounded lophs (Korth, 1994a). The lowers of tree squirrels and tamiines may be distinguishable by being rectangular or square in outline, while the ground squirrels have lower cheek teeth with a rhombic occlusal outline due to a shorter lingual margin than buccal margin (Black, 1963).

The flying squirrels (Pteromyinae) are most recognizable by the rugose enamel of the basins of the teeth, as well as strongly convergent or parallel lophs in the upper teeth, and well-developed entoconids (de Bruin, 1999) except for *Blackia* and *Sciurion* (Mein, 1970; Skwara, 1986; de Bruin, 1999).

6.1 SYSTEMATIC PALEONTOLOGY

SCIURIDAE Gray 1821

PTEROMYINAE Brandt 1855

SCIURION Skwara 1986

Type species—*Sciurion campestre* Skwara, 1986

Referred species—*Sciurion xenokleitus* sp. nov.; *Sciurion oligocaenicus* sp. nov.

Age and Distribution—Orellan, Whitneyan, Arikareean and Hemingfordian of southwest Saskatchewan; Clarendonian of Nebraska.

Emended Diagnosis—Small to medium sized pteromyines (m1/2 is 1.3 mm to 1.6 mm long); differs from *Petauristodon* in lacking protoconule, metaconule, and accessory lophs; differs from *Blackia* in presence of anteroconid, mesoconid, and (incipient) hypocone. Other distinguishing characters include: enamel of basins of teeth finely crenulated when unworn, high relief on occlusal surface of teeth; molar structure simple. Upper cheek teeth lacking conules or accessory lophs; protocone narrow anteroposteriorly; P4 with or without mesostyle on mesostylar ridge; when present, mesostyle may be reduced or well developed; M1 or M2 with strong mesostyle; variably developed hypocone and parastyle; M3 smaller than M1 or M2. Lower cheek teeth bearing anteroconid and mesoconid, mesoconid better developed on molars than premolar; hypoconid strong, displaced buccally resulting in an enlarged talonid; mesostylid distinct on m1 or m2, incorporated into high cingulum on p4. This diagnosis is essentially the same as that of Skwara (1986) except for the increase in size range within the genus and the reference to the variability of the mesostyle on P4.

Discussion—The species *Sciurion xenokleitus* and *S. oligocaenicus* have also been recovered in the Orellan Fossil Bush Locality (Meyer, 2003) and the Arikareean-age Kealey Springs Local Fauna (Storer, 2002); both of these sites also occur in the Cypress Hills Formation of Saskatchewan. Korth (1998b) described a single tooth of this genus from the late Clarendonian Ash Hollow Formation of Nebraska.

SCIURION OLIGOCAENICUS SP. NOV.

Table 6.1, Figure 6.3 a-f

Holotype—SMNH P2840.142 (Lp4), Fossil Bush Local Fauna, Cypress Hills Formation (Orellan).

Referred specimens from Rodent Hill —SMNH P2452.123 (RdP4); P2521.283 (LP4); P2834.005 (LM1 or M2); P2521.259 (Rdp4); P2521.304 (Ldp4); P2521.188 and P2521.338 (Lp4), P2521.060 (Rp4), P2521.202 (Rm1 or m2), P2521.253 and P2521.272 (Lm1 or m2), and P2521.382 (Lm3).

Horizon at Rodent Hill —P2834.005 from Stratigraphic Unit I. Other specimens collected in stratigraphically uncontrolled sampling.

Diagnosis— Similar in overall size to *S. campestre*, but more robust; about 25% smaller than *S. xenokleitus*. P4/p4 and M3/m3 enlarged relative to those of *S. campestre*; proportions of p4 and m1-2 longer than wide (TR/AP<1) compared to proportions in *S. campestre* (TR/AP>1); proportions of m3 similar in length and width (TR/AP≤1) whereas the m3 of *S. campestre* is much longer than wide (TR/AP<<1); cusps more bulbous and lophs thicker than in *S. campestre*.

Description— The deciduous upper premolar is identified based on comparisons with those described for *Blackia* (DeBruijn and Ünay, 1989). The D4 has a broad triangular outline due to the expansion of the anterior transverse valley and anterocone. The paracone is large, triangular in shape and somewhat anteroposteriorly compressed, and extends into the straight protoloph directly to the anterior margin of the protocone. At the buccal end of the central transverse valley is a very low, buccally expanded mesostyle. The metacone is smaller than the paracone but they are subequal in height. The metaloph is complete and curves anterobuccad to the protocone. On the posterior margin of the tooth a very low posterior cingulum is present that is only very narrowly separated from the raised metaloph that extends from the metacone to the minute and somewhat distinct hypocone.

The P4 is triangular in outline, with a more acute angle at the protocone than the DP4. The anterior margin of the tooth expands anteriorly, particularly at the anterocone. The anterior transverse valley is wide but steeper-walled and lower than the central transverse valley. The paracone is high and anteroposteriorly compressed, and extends to the protocone via a protoloph that does not bear any conules. The protocone is about as high as the paracone, and is very transversely compressed. The central transverse valley has a number of crenulations, and buccally is interrupted by a large mesostyle; the mesostyle joins to the paracone by a low, narrow loph. The metacone is slightly lower than the paracone and more anteroposteriorly compressed, and does not join to the mesostyle. The metaloph is roughly parallel and equal in height to the protoloph, and also lacks any conules. Posterad to the metaloph is a narrow posterior transverse valley, which is enclosed posteriorly by a low posterior ridge. At the lingual-most end of the posterior ridge is a small, ovate hypocone.

The M1 or M2 has a slightly rhomboidal outline and no fine enamel crenulations are visible on the very worn occlusal surface. The protocone dominates the lingual margin, is anteroposteriorly narrow and is located anterior of center. The paracone is narrow and higher in relief than the metacone, and is connected to the protocone by a low protoloph that is parallel to the anterior margin. The metacone connects to the protocone with a low metaloph that transverses the occlusal surface from the metacone anterolingually to the protocone. Both the protoloph and metaloph exhibit very narrow expansions about midway along their length, which could be interpreted as a reduced protoconule and metaconule, but are more likely a result of tooth wear. The hypocone is poorly developed but clearly visible on the posterior margin; it joins with the metacone by a shallow posterior cingulum that is interrupted midway by the metaloph. The broad, low anterior cingulum is higher at the buccal than the lingual margin. A poorly developed parastyle is separated by a shallow depression from the paracone while a deeper notch separates the lingual margin of the cingulum from the protocone. The mesostyle is very worn, but present, and strongly connected to the paracone, but is not attached to the metacone.

The dp4 (P2521.304, P2521.259) were identified based on comparisons with a *Blackia* dp4 figured in de Bruijn and Ünay (1989). These teeth have a somewhat quadratic occlusal outline, longer than a p4, and shorter than m3. The teeth are worn, with only a few remnant lophules present in the posterior of the basin that suggest the enamel rugosity characteristic of *Sciurion*. The metaconid is the highest cusp of the tooth, and joins to the protoconid via metalophulid I. The well-developed anteroconid is present that is slightly closer to the protoconid. Posterior to the anteroconid is a small

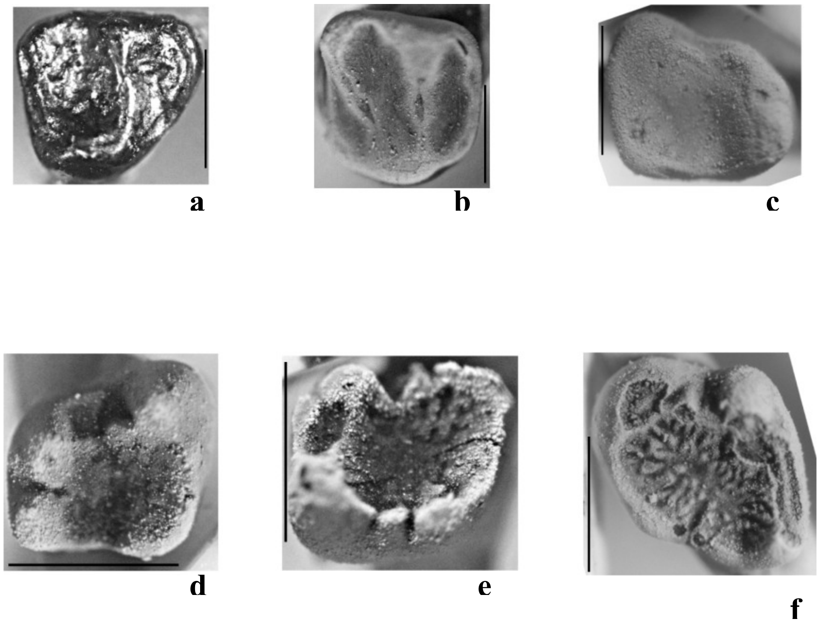


Figure 6.3 *Sciurion oligocaenicus*: a. SMNH P2452.123 RD4; b. SMNH P2834.005 RM1-2; c. SMNH P2521.304 Ld4; d. SMNH P2521.060 Rp4; e. SMNH P2521.202 Rm1-2; f. SMNH P2521.382 Lm3. Scale = 1mm, buccal to top of page.

fossettid indicating the enclosed trigonid basin. The entire trigonid is much higher than the talonid. Joining the protoconid to the very low hypoconid is a very poorly developed ectolophid. Buccal to the ectolophid is a narrow, but deep buccal shelf with no apparent mesoconid. The hypoconid is slightly expanded buccally, and joins to the entoconid by a low posterolophid. A small swelling in the posterolophid is present just lingual of the hypoconid. Anterior to the entoconid there does not appear to be any mesostylid or metastylid crest.

The p4 has a trapezoidal occlusal outline, and although the basins are worn on all specimens, some rugosity is still visible as very low lophules (P2521.188) or low crenulations (P2521.060 and P2521.338). The anterior margin of the tooth is transversely compressed relative to the posterior margin, and the metaconid is wider and higher than the protoconid. The anteroconid is poorly developed and closely appressed to the protoconid. The trigonid basin is short, being closed off from the talonid by a short metalophulid II on P2521.060 and P2521.338 (indistinguishable on P2521.188), and the trigonid is high relative to the talonid. A poorly developed mesoconid is present on the low ectolophid that is present close to the buccal margin of the tooth. Buccal to the ectolophid is a shallow metastylar shelf. The hypoconid is wide, lower in height than the protoconid, and appears expanded buccally, causing the talonid to be buccolingually wider than the trigonid. A shallow posterolophid is evident that is highest at the hypoconid and the posterolingual margin. The entoconid is present as a very minor widening at this margin. A small mesostylid is present only on the metastylid crest of P2521.338, and is separated by a narrow gap from the entoconid

The m1 or m2 has a quadrate occlusal outline. The enamel crenulations are well developed on P2521.253, but are barely distinguishable on P2521.2020 and P2521.72. These teeth vary in the amount of relative transverse compression of the anterior cusps, from closely appressed on P2521.253 to more widely spaced in P2521.272, but this range of variation is considered here to be acceptable until more material of this genus becomes available for comparison. A very small trigonid basin, that is slightly higher than the talonid basin, is variably enclosed by metalophulid II. The low ectolophid is set

Table 6.1 Dental measurements of *Sciurion oligocaenicus*.

Tooth position	Dimension	N	Mean	OR
D4	AP	1	1.45	
	TR	1	1.33	
P4	AP	1	1.23	
	TR	1	1.25	
M1-2	AP	3	1.10	
	TR	3	1.30	
d4	AP	2	1.35	1.33-1.38
	TRA	2	1.13	1.03-1.23
	TRP	2	1.09	0.93-1.25
p4	AP	3	1.14	1.08-1.20
	TRA	3	0.87	0.80-0.93
	TRP	3	1.03	0.93-1.10
m1	AP	1	1.30	
	TRA	1	0.93	
	TRP	1	1.25	
m2	AP	2	1.24	1.20-1.28
	TRA	2	1.06	1.03-1.10
	TRP	2	1.25	1.20-1.30
m3	AP	1	1.50	
	TRA	1	1.45	
	TRP	1	1.35	

well in from the buccal margin of the tooth, with a well-developed mesoconid that is set closer to the hypoconid. The hypoconid is broad and expands buccad to the protoconid, particularly in P2521.253, causing the talonid to be buccolingually wider than the trigonid. The posterolophid is higher than the talonid valley, but lower than the trigonid, and is highest at the hypoconid; at the lingual margin, the posterolophid becomes lobate and terminates in a poorly developed entoconid. The mesostylid is separated from the entoconid by a notch, and rests about midway along the lingual margin of the tooth. A low metastylid crest extends posteriorly from the metaconid and does not join to the mesostylid.

The occlusal outline of m3 is slightly rhombic, and longer anteroposteriorly. The metaconid is high and almost conical, much higher than the protoconid that is low, wide and posteriorly offset to the metaconid. Most of the anterior margin is damaged or worn away, making assessment of the anterior portion of the m3 difficult. From what is visible the anteroconid is low and poorly defined, present as a swelling anterolingually to the protoconid and connected to the metaconid by a low metalophulid I. The trigonid basin is open posteriorly and higher than the talonid. A well-developed mesoconid on a poorly developed ectolophid is set lingually of the buccal margin, and is separated from the protoconid and hypoconid by deep notches. The hypoconid is wide and dominates the posterolophid. The posterolophid runs diagonally from hypoconid to the lobate posterolingual corner, where a slight expansion represents the entoconid. A deep notch separates the entoconid from the weak mesostylid. A very low metastylid crest posterad to the metaconid extends to the mesostylid, but they are separated by a very shallow gap.

Discussion—The species *Sciurion oligocaenicus* was described by the author and Taran Meyer while reviewing the Saskatchewan pteromyines. This is the smaller of two new species described from the Oligocene of Saskatchewan. Specimens of this species have also been described from the Orellan-age Fossil Bush Locality (Meyer, 2003) as *Sciurion* "new species" and from the early Arikareean-age Kealey Springs Locality (Storer, 2002) as either *Protosciurus* sp. or *Nototamias* sp. It is similar in appearance to the Hemingfordian-age *Sciurion campestre*, but appears to be a more robust species, with relatively larger premolars and third molars, and heavier cusps, lophs and crenulations. It is reasonable to infer that *S. oligocaenicus* may represent an ancestor to *Sciurion campestre*. There appears to be a general reduction in the length of the lower teeth from the Fossil Bush *S. oligocaenicus* to the *S. oligocaenicus* of Kealey Springs. This trend would grade into the tooth proportions seen in *S. campestre*, but the small number of specimens from all four sites makes it unclear whether this trend is statistically valid, or is a reflection of individual variations. It is also possible that what appears to be a general trend within the *S. oligocaenicus* specimens from Fossil Bush, Rodent Hill and Kealey Springs may actually indicate separate species from each site, but at the moment they appear to share sufficient morphology with each other to warrant grouping into one species that is distinct from *S. campestre*.

SCIURION XENOKLEITUS SP. NOV.

Table 6.2, Figure 6.4

Holotype—SMNH P2452.126 (Lm1), Rodent Hill Locality, Cypress Hills Formation, Saskatchewan (Whitneyan).

Referred specimens from Rodent Hill —SMNH P2836.007 (RdP4); P2521.033, P2521.047, P2521.333, P2834.004 and P2834.014 (RM1 or M2); P2452.122, P2835.004, P2836.006 and P2836.010 (LM1 or M2); P2452.124 and P2452.125 (RM3); P2835.001 (LM3); P2521.082 and P2521.083 (Rm1-2); P2452.126 (Lm1-2); P2835.003 (Rm3) and P2521.322 and P2785.020 (Lm3).

Etymology—*XENO-*, (Gr.) foreign, strange; *-KLEITUS*, (Gr.) hillside, slope; refers to the unexpected occurrence of this genus at the Rodent Hill Locality, a site on a hillside.

Horizon at Rodent Hill —SMNH P2834.004 and P2834.014 from Stratigraphic Unit I, P2835.003 and P2835.004 from Stratigraphic Unit II, and P2836.006 and P2836.010 from Stratigraphic Unit V. All others collected in stratigraphically uncontrolled sampling.

Diagnosis—Morphologically very similar to *S. campestre* but 25% larger. Anteroconid of m1/m2 well developed, but less pronounced than in *S. campestre*; entoconid of m1-m3 present, often well developed, unlike in *S. campestre*.

Description—Like the smaller species of *Sciurion* and many other pteromyines, the basins of unworn teeth bear numerous fine crenulations Except for the dP4, which is broadly triangular, the upper cheek teeth are generally rhomboid to trapezoidal in outline and bear a protocone that is anteroposteriorly compressed. The lowers are quadrate to trapezoid in occlusal outline, and the hypoconid is expanded buccally causing the talonid to be wider than the trigonid. In the lower cheek teeth the m3 is longer anteroposteriorly than m1 or m2, and only slightly wider.

The dP4 has a triangular outline due to the expansion of the anterocone, which is slightly raised above the anterior transverse valley. The anterior transverse valley is wide and V-shaped. The paracone is prominent on the buccal end of the protoloph, situated slightly lingually from the buccal margin, and round. The protoloph extends uninterrupted to the anterior end of the protocone crest. The central transverse valley is about as wide as the anterior transverse valley, but is more U-shaped. The mesostyle is isolated and prominent, blocking the buccal end of the central transverse valley, and has a mesostylar ridge that extends about one third of the way into the valley. The metacone is round, smaller and lower than the paracone, and is connected with the posterior edge of the protocone by an uninterrupted metaloph that is slightly curved and subparallel to the protoloph. The buccal portion of the posterior transverse valley is narrower, and a low ridge (not substantial enough to be considered a cingulum) is present posterad to the posterior transverse valley. At the posterior margin, posterad to the protocone crest, a swelling is present that may be a hypocone. The enamel of all three transverse valleys is worn, but the crenulations and lophules are clearly present.

The M1 or M2 are rhomboidal in outline although some appear slightly more trapezoidal. The protocone occupies more than half of the lingual margin and occurs slightly anterad of center. The paracone and metacone are narrow and elevated, the paracone occurring lingual to the buccal margin. The metacone and paracone connect to the protocone via subparallel lophs that lack conules and accessory lophs. The well-developed mesostyle occurs beside the paracone and is separated from the metacone. The hypocone is poorly developed in some specimens and not present in others. The hypocone connects buccolingually to the metacone via a low posterior cingulum. The wide, low anterior cingulum is separated from the protocone by a notch, which may be more pronounced in M2, and buccally rises into a low crest that may bear a poorly developed parastyle.

M3 is slightly larger than M1 or M2 and triangular in outline. The large protocone dominates the lingual margin of the tooth. The narrow, elevated paracone connects to the protocone via a low and wide protoloph that runs parallel to the anterior cingulum. The anterior cingulum is low and separated from the paracone by a shallow notch but connects directly to the anterior margin of the protocone. The central transverse valley is expanded into a broad basin that is bounded posteriorly and lingually by a low crest. The metacone is present as a widening in the posterobuccal-most corner of the crest. The crest terminates at the small mesostyle that is present as a small cuspule posterior to the paracone.

The m1 or m2 has a slightly trapezoidal occlusal outline, with the trigonid slightly narrower than the talonid. The enamel crenulations in the talonid basin vary, from fewer, thicker lophules (P2521.082) to larger numbers of thinner lophules (P2521.126). This difference may result from wear of the enamel. The metaconid is higher than the anteroposteriorly-compressed protoconid, and is set slightly anterad. The anteroconid is low and broad, not as pronounced as in *S. campestre*, and connects to the metaconid by a rising metalophulid I, while separated by a deep notch from the protoconid. A short metalophulid II extends lingually from the protoconid; this loph may extend across the trigonid, or only reach part way across the basin. A poorly developed mesoconid is present on the low ectolophid that joins the protoconid and

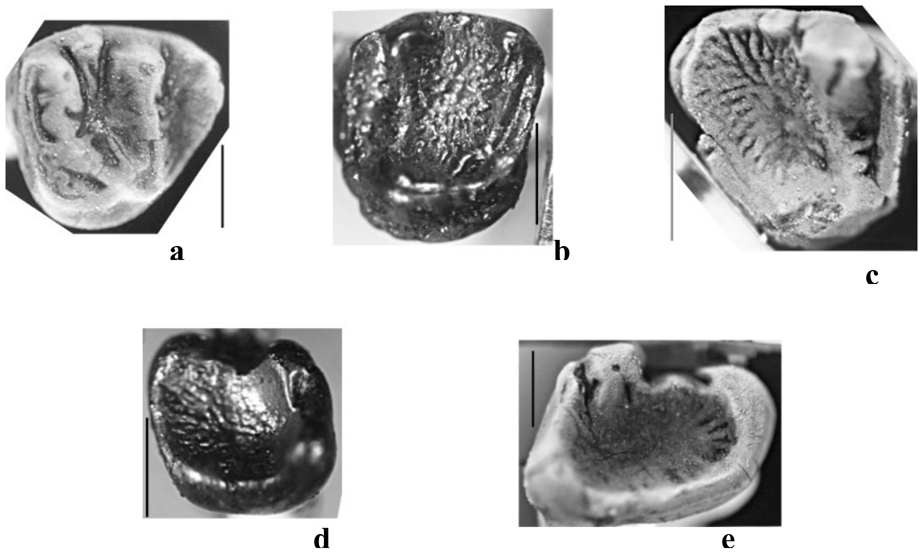


Figure 6.4 *Sciurion xenokleitus*: a. SMNH P2836.007 RD4; b. SMNH P2834.004 LM1-2; c. SMNH P2835.001 RM3; d. SMNH P2452.126 Lm1-2; e. SMNH P2835.003 Rm3. Scale = 1mm, buccal to top of page.

hypoconid. There are small internal inflections of the ectolophid anterior to the hypoconid and posterior to the protoconid. The hypoconid is slightly lower than the protoconid and is buccally expanded relative to the protoconid, causing the buccal expansion of the talonid. The posterolophid is well developed but lower than the posterior cusps, and joins to the well-developed entoconid at the posterolingual corner of the tooth. The mesostylid is low but well developed, and is separated by a deep notch from the entoconid, and by a shallower notch from the metastylid crest that extends from the metaconid.

The occlusal outline of m3 is trapezoidal and extended anteroposteriorly. The metaconid is very high and anteroposteriorly compressed. The protoconid is lower and wider and placed slightly posteriorly to the metaconid. The anteroconid is broad and anteroposteriorly narrow, and joins to the metaconid by a low anterior lophid while separated from the protoconid by a deep notch. The trigonid is not enclosed posteriorly by any lophids and is slightly raised above the talonid. The ectolophid is set near to the buccal margin of tooth, with a small, variably developed mesoconid. Buccal to the ectolophid is a deep and narrow buccal shelf. The ectolophid is straight and joins the hypoconid and the protoconid. The hypoconid is broad, lower than and slightly expanded buccad to the protoconid. The posterolophid is low, almost diagonal from the hypoconid to the mesostylid, and slightly lobate at the posterolingual edge, which may be angular or smoothly curved. The entoconid is variably present as either a small but well-developed cusp (P2785.020), a distinct swelling on the lingual edge of the posterolophid (P2521.322) or as a very slight swelling that is subsumed into the posterolophid (P2835.003). On P2835.003, the posterolophid then continues around to the lingual edge, eventually terminating at the metaconid and leaving no visible mesostylid. On the other specimens, the posterolophid ends at the entoconid, and the mesostylid, which varies in size, is separated from the entoconid and metastylid crest by narrow notches.

Table 6.2 Dental measurements of *Sciurion xenokleitus*. Holotype SMNH P2452.126 (Lm1-2).

Tooth position	Dimension	N	Mean	OR	SD	CV	Holotype
D4	AP	1	1.90				
	TR	1	1.80				
M1-2	AP	9	1.83	1.75-1.90	0.07	3.61	
	TR	9	2.01	1.80-2.20	0.14	7.17	
M3	AP	3	1.91	1.88-1.98			
	TR	3	2.06	2.00-2.15			
m1-2	AP	3	1.73	1.70-1.78			1.78
	TRA	3	1.62	1.55-1.65			1.65
	TRP	3	1.80	1.68-1.95			1.95
m3	AP	3	2.02	1.88-2.18			
	TRA	3	1.88	1.78-1.98			
	TRP	3	1.56	1.48-1.70			

Discussion—*Sciurion xenokleitus* is the second species referred to the genus *Sciurion*, and except for a substantial difference in size (25% larger) is morphologically very similar to the genotype. There are many more specimens of *S. xenokleitus* than of *S. oligocaenicus* in the Rodent Hill Local Fauna. Specimens representing this species have been identified from the Orellan Fossil Bush Locality and the Arikareean Kealey Springs Fauna (Meyer, 2003; Storer, 2002).

CEDROMURINAE Korth and Emry 1991

CEDROMUS Wilson 1949

Type species—*Cedromus wardi* Wilson, 1949

Referred species—*C. wilsoni*, Korth and Emry, 1991

Age and distribution—Orellan of Wyoming, South Dakota, Colorado and Nebraska; Whitneyan of Nebraska and Saskatchewan.

Diagnosis—Larger than *Oligospermophilus*; hypocones small and metaconule large on upper molars; mesostyle close to metacone on upper molars, completing ectoloph from mesostyle to metacone, blocking central transverse valley buccally with wear; posterior cingulum continuous with entoconid and mesostylids buccolingually elongate on lower molars. From Korth and Emry (1991).

CEDROMUS SP. CF. *C. WILSONI* Korth and Emry 1991

Table 6.3, Figure 6.5

Holotype—USNM 256584, complete skull with all teeth except P4s, Orella member, White River Formation, Wyoming (Orellan).

Referred specimen from Rodent Hill —SMNH P2836.003 (LM 1 or 2).

Horizon at Rodent Hill —Stratigraphic Unit V.

Diagnosis—Smaller than *C. wardi*; ectoloph incomplete, continuous from paracone to mesostyle on P4-M3, not connecting with metacone; metaconule variably continuous with protocone by narrow connection; hypolophid more strongly developed than in type species, commonly continuous with ectolophid; anterostylid variably

Figure 6.5 *Cedromus* cf. *C. wilsoni*: SMNH P2836.003 LM1-2. Scale = 1mm, buccal to top of

present on p4. From Korth and Emry (1991).

Description—The tooth is a very worn specimen so most occlusal features are faint. P2836.003 is equal length anteroposteriorly to *Cedromus wilsoni* specimens previously described by Korth and Emry (1991), but is slightly narrower buccolingually (14% difference). The paracone is very high relative to the occlusal surface, and a very small protoconule is present as a widened area on the protoloph. The buccal margin of the paracone extends posterad as a narrow ectoloph that terminates at a small mesostyle that is located close to the metacone. The metacone is worn but clearly present as a large round depression on the buccolingual corner of the tooth, while the metaloph is worn to a very low ridge. A large metaconule is present as a depression that is lingual to the metacone, and no hypocone is present due to wear. The anterior cingulum is low and ends buccally in a small parastyle that is worn to give the appearance of a slight anterobuccal expansion.

Table 6.3 Dental measurements of *Cedromus* cf. *C. wilsoni*.

Tooth position	Dimension	N	Mean
M1-2	AP	1	2.33
	TR	1	2.60

Discussion—The large metaconule, larger size, and presence of an ectoloph are the main reasons that this specimen has been placed in the genus *Cedromus* instead of *Oligospermophilus*. P2836.003 shares the incomplete ectoloph that distinguishes *C. wilsoni* from *Cedromus wardi*, as well as the smaller size. A problem with the assignment is that only one specimen was recovered, an M1 or M2 that is very worn, with features that are difficult to distinguish. P2836.003 is also 14% smaller than the *C. wilsoni* specimens described by Korth and Emry (1991), but the apparent morphological similarities between P2836.003 and previously described *C. wilsoni* specimens probably suggest a variation of size within the species, as opposed to a distinct species.

SCIURINAE Gray 1821

TAMIINI Black 1963

NOTOTAMIAS Pratt and Morgan 1989

Type species—*Nototamias hulberti* Pratt and Morgan 1989.

Referred species—*N. quadratus* Korth 1992b.

Age and distribution—Whitneyan of Saskatchewan; Arikareean of Nebraska, South Dakota and Saskatchewan; Hemingfordian of Florida.

Dental diagnosis—Fused anterior and posterior roots on lower molars; anterolabial groove on lower cheek teeth reduced or lost; loss of mesoconid on the lower cheek teeth. From Pratt and Morgan (1989).

NOTOTAMIAS SP.

Table 6.4, Figure 6.6

Referred specimens from Rodent Hill —SMNH P2521.080 (Lp4), P2521.294 (Lm1/2).

Horizon at Rodent Hill —Specimens collected in stratigraphically uncontrolled sampling.

Description— This is a very small sciurid species, roughly equal in size to *Sciurion campestre*. The teeth show no crenulations. The teeth increase marginally in size from the p4 to the m1.

The p4 has a trapezoidal occlusal shape, with a wider and slightly higher metaconid than protoconid; these cusps are joined by a lower anterolophid, and there is no anteroconid. The hypoconid is wide and low, and expands buccad to the protoconid, causing the talonid to be buccolingually wider than the trigonid. A well-developed

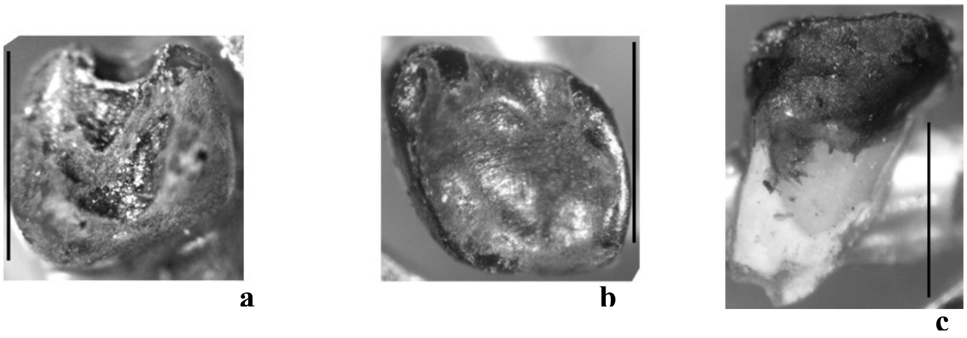


Figure 6.6 *Nototamias* sp.: a. SMNH P2521.081 Lp4; b. SMNH P2521.294 Lm1-2; c. SMNH P2521.294 (posterior). Scale = 1mm, buccal of a,b to top of page.

ectolophid, lacking any mesoconid, joins the hypoconid and protoconid and is located well lingual of the buccal margin of the tooth. No posterolophid is evident, and the hypoconid joins to the much higher entoconid by a low, narrow posterior cingulum. A partial hypolophid extends from the entoconid about halfway across the posterior margin. The entoconid is well developed and about the same height as the metaconid. No mesostylid is present between the two lingual cusps. Across the center of the tooth, extending anterobuccally from the entoconid to the protoconid is a raised loph that cuts diagonally across the talonid basin.

The m1/2 has a rhombic occlusal outline, and is a very worn specimen. The metaconid appears to be about the same height as the protoconid, with the two cusps connected by a narrow metalophulid I. The trigonid basin is very narrow and appears to be partially closed posteriorly by a very narrow metalophulid II. The hypoconid is low and buccally expanded, causing the talonid to be somewhat wider than the trigonid. The ectolophid is clearly visible, although no mesoconid is apparent. The hypoconid extends into the posterolophid lingually, which reaches the low but distinct entoconid. The mesostylid is faint, but this may be due to wear. The anterior roots are broken away, but the posterior roots are present almost to their tips, and are clearly fused together. Only at the very tip is there any indication of separation between these roots.

Table 6.4 Dental measurements of *Nototamias* sp.

Tooth position	Dimension	N	Mean
p4	AP	1	1.08
	TRA	1	0.88
	TRP	1	1.10
m1-2	AP	1	1.03
	TRA	1	1.03
	TRP	1	1.05

Discussion—These specimens are among the smallest sciurids found at the Rodent Hill Locality, and cannot be referred to any known contemporary taxon. The very small size is reminiscent of *Sciurion oligocaenicus*, but these specimens lack many of the typical features of those taxa, such as the crenulated enamel and the anteroconid.

In both size and morphology these two teeth are very reminiscent of the *Nototamias* figured by Storer (2002) and are definitely referable to the genus based on the dental diagnosis given by Pratt and Morgan (1989). The most compelling evidence, along with the small size of the Rodent Hill specimens, is the lack of the mesoconid and the fused roots of the m1. The surface of the m1 is too worn to preserve the area of the anterolabial groove, so its presence can be neither confirmed nor denied. The very pronounced entoconid of the p4 is unusual but a large entoconid is present on the p4 in the specimens of *N. quadratus* described by Korth (1992b). Of the described species of *Nototamias,* the Rodent Hill specimens are smaller but closer in size to *N. hulberti* based on the dimensions given by Pratt and Morgan (1989), particularly the p4. Since only two worn specimens of this population have been recovered, no assignment to species can be made.

MARMOTINI Pocock 1923

PROTOSPERMOPHILUS Gazin 1930

Type species—*Citellus (Protospermophilus) quatalensis* Gazin, 1930

Referred species—*P. vortmani* (Cope, 1879); *P. malheurensis* (Gazin, 1932); *P. angusticeps* (Matthew and Mook, 1933); *P. oregonensis* (Downs, 1956); *P. kellogi* (Black, 1963).

Age and distribution—Whitneyan to Barstovian (possibly Clarendonian) of western North America.

Diagnosis—Skull slightly convex dorsally; cranium moderately expanded; dorsal limit of zygomatic plate terminating on side of rostrum; masseteric tubercles small; notches in ventral border of zygomatic plate opposite either m1 or line of contact between p4 and m1; masseteric fossa deeply concave, ending below m1; generally a small pit anterior to masseteric fossa for separate slip of masseter; cheek teeth low crowned but robust; protoconules absent or subordinated in protolophs, metaconules distinct; protocone-posterior cingulum union expanded; entoconid a distinct cusp; entoconid corner angular. Emended by Black (1963).

PROTOSPERMOPHILUS SP.

Table 6.5, Figure 6.7

Referred specimens from Rodent Hill—SMNH P2521.362 (Lm2); P2452.127 (Rm3).

Horizon at Rodent Hill—Collected in stratigraphically uncontrolled sampling.

Description—This m2 is worn and some features are not clearly visible. The tooth has a rhomboidal occlusal outline and is wider than it is long. The metaconid is

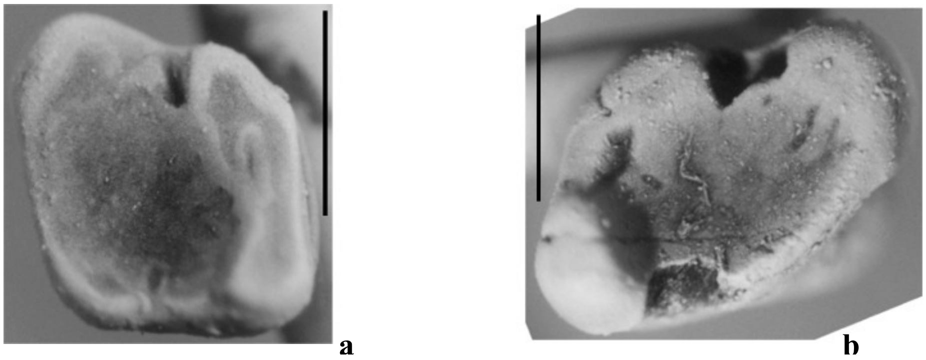


Figure 6.7 *Protospermophilus* sp.: a. SMNH P2521.362 Lm2; b. SMNH P2452.127 Rm3. Scale = 1mm, buccal to top of page.

well developed and higher than the protoconid. A very shallow anterior cingulum is visible, as well as a metalophid extending from the protoconid to the midpoint of the anterolophid, partially enclosing the trigonid basin; the trigonid is higher than the talonid. The ectolophid is worn, set lingually from the buccal margin and is very low. The mesoconid is a small, round cuspule midway along the ectolophid. The hypoconid is low and buccally expanded, and is connected to the entoconid by a very low posterior ridge. The entoconid is well developed and higher than the hypoconid, but is not as high as the metaconid. On the lingual edge a mesostylid is not clearly present, but a low metastylid ridge that is interrupted anteriorly to the entoconid extends posteriorly from the metaconid.

The very curved posterolingual margin causes the occlusal outline of the m3 to appear rhombic. The tooth is larger than the m2, being longer anteroposteriorly, and is the same width. The metaconid is bulbous and much higher than the protoconid, and these cusps are connected by a low metalophulid I. The trigonid basin is enclosed by a metalophulid II that extends from the protoconid to the metaconid and is slightly raised above the talonid. The hypoconid is about the same size and height as the protoconid, with the two connected by a low ectolophid that lacks a mesoconid. On the anterior face

Table 6.5 Dental measurements of *Protospermophilus* sp.

Tooth position	Dimension	N	Mean
m2	AP	1	1.43
	TRA	1	1.50
	TRP	1	1.63
m3	AP	1	1.80
	TRA	1	1.63
	TRP	1	1.25

of the hypocone are two shallow grooves, possibly remnants of enamel rugosity. A deep buccal shelf is present buccad to the ectolophid. A low posterolophid extends from the hypoconid to the posterolingual margin of the tooth. No entoconid is clearly present because the lingual margin appears to have been worn away during transport. In front of the lingual terminus of the posterolophid is a buccally directed gap in the tooth produced by breakage that extends to the posterior margin of the metaconid.

Discussion—These two specimens are indicative of lower cheek teeth of marmotines and ground squirrels as diagnosed by Black (1963) in their shorter lingual than buccal margins, the rhomboidal shape of the m2, and the high posterolophid of P2452.127. The entoconid of P2521.362 is better developed than indicated by Black (1963) for later marmotines, but a distinct entoconid is a diagnostic feature for *Protospermophilus* (Black, 1963).

These *Protospermophilus* specimens may be the oldest known record of this genus so far, and would be the smallest. This is in line with a general increase in size of the genus over time from the Arikareean *Protospermophilus vortmani* to the latest species of the Barstovian or Clarendonian, based on dimensions given by Black (1963). Of the taxa included by Black in the genus *Protospermophilus*, SMNH P2521.362 most resembles an indeterminate Arikareean specimen referred to as *Protospermophilus* sp (Black, 1963, pp. 162). The major difference is that the Rodent Hill specimens are smaller, do not have a definite mesostylid, and there is only minimal talonid rugosity present in P2452.127, and none in P2521.362. These latter two features are probably indeterminate due to wear. With only two specimens available it is difficult to draw any other conclusions regarding the evolutionary or biogeographic history of this genus, or to make any definitive designations of the species.

7. FAMILY CASTORIDAE

The Castoridae includes the modern beavers, *Castor canadensis* of North America and *C. fiber* from Eurasia (Korth, 1994a). The ancestral rodent family to the beavers remains unknown, although there are possibilities within the Paramyidae or Ischromyidae (Korth, 1994a). The earliest North American beaver known is *Agnotocastor galushai* from middle Chadronian localities although the earliest Eurasian species are roughly the same age (Korth, 1994a). North American beavers reached a peak of diversity in the Arikareean, and experienced a second radiation in the Blancan, from which the modern *Castor* is descended (Korth, 1994a).

The castorids have a sciurognathous jaw angle and, where known, are sciuromorphous (Korth, 1994a).

The dental formula for castorids is 1013/1013 except for agnotocastorines, which still retain at least P3 (Korth and Emry, 1997). Early beavers have cheek teeth that are mesodont, although many later genera develop fully hypsodont teeth. The P4/p4 is the largest tooth in the tooth row, and there is a general decrease in size to the M3/m3 (Korth, 1994a). Due to unique adaptations of castorid dentition, the cusps of the teeth are very difficult to identify (Korth, 1994a). Instead, the teeth are described based on the presence and morphology of enamel lakes (fossette/-id) or reentrant enamel valleys (flexus/-ids) that were named, based on relative tooth position, by Stirton (1935). On the lateral enamel of the teeth there may be vertical reentrant enamel folds referred to as stria/-ids that correspond to the flexi.

In the upper teeth (**Figure 7.1**), the anterior-most buccal fossette is the parafossette, the medial fossette is the mesofossette, and posterior-most is the metafossette. The only lingual fossette is the hypofossette. If these enamel lakes open

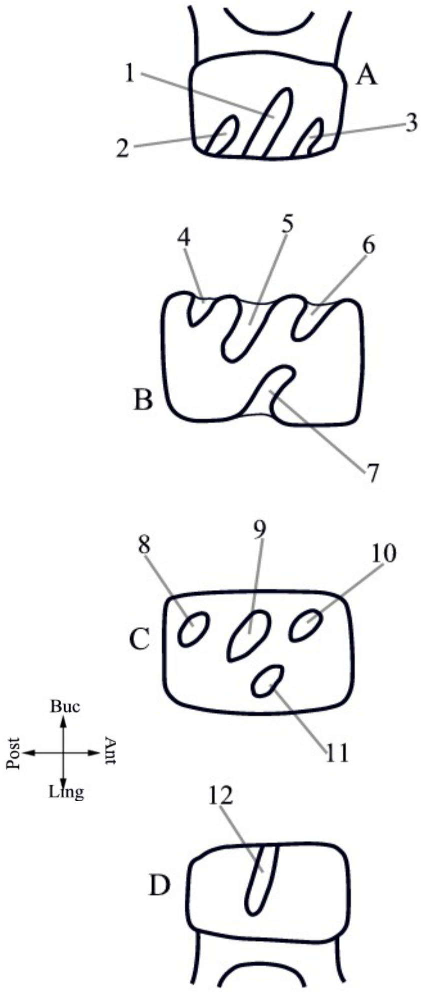


Figure 7.1 Generalized castorid upper cheek tooth morphology with major features identified. A—Buccal view (occlusal down) B, C—Occlusal view D—Lingual view (occlusal up). 1–mesostria 2—metastria 3—parastria 4—metaflexus 5—mesoflexus 6—paraflexus 7—hypoflexus 8—metafossette 9—mesofossette 10—parafossette 11—hypofossette 12—hypostria

Drawn by the author, based on Korth (2001b). Terminology from Stirton (1935).

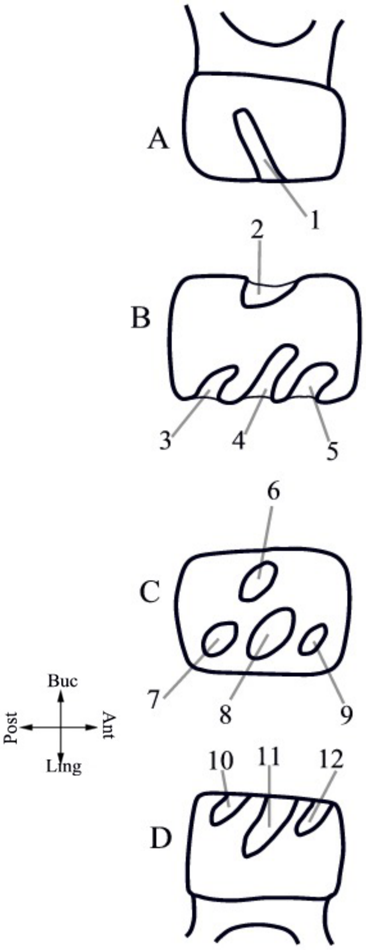


Figure 7.2 Generalized castorid lower cheek tooth morphology with major features identified. A—Buccal view (occlusal down) B, C—Occlusal view D—Lingual view (occlusal up). 1–hypostriid 2—hypoflexid 3—metaflexid 4—mesoflexid 5—paraflexid 6—hypofossettid 7—metafossettid 8—mesofossettid 9—parafossettid 10—metastriid 11—mesostriid 12—parastriid

Drawn by the author, based on Korth (2001b). Terminology from Stirton (1935).

to the margins of the tooth to form reentrant valleys, they are described as flexi (Stirton, 1935; Korth, 1994a).

The anterior-most lingual fossettid of the lower teeth (**Figure 7.2**) is the parafossettid, followed by the mesofossettid and the posterior-most fossettid is the metafossettid. On the buccal margin is the hypofossettid. If the fossettids open to the margins of the teeth, they are referred to as flexids.

In several species of castorids, there may be other distinct enamel lakes present on the occlusal surface that could be used for identification. Xu (1996) determined that the identification of beavers solely on dentition is unreliable, so the identifications made here will be tentative. Castorids in the subfamily Agnotocastorinae can be recognized dentally by having mesodont teeth (Korth and Emry, 1997) with a more complex occlusal pattern (Korth and Emry, 1997; Korth, 2001b). The Palaeocastorinae are recognizable dentally by having a simplified occlusal pattern and molars that are higher crowned but still rooted (Korth, 2001b).

7.1 SYSTEMATIC PALEONTOLOGY

CASTORIDAE Hemprich, 1820

AGNOTOCASTORINAE Korth and Emry, 1997

AGNOTOCASTOR Stirton, 1935

Type species—*Agnotocastor praetereadens* Stirton, 1935

Referred species—*A. coloradensis* Wilson, 1949; *A. galushai*, Emry, 1972; *A. auabekerovi,* Lytshev, 1978; *A. readingi*, Korth, 1988

Age and distribution—Chadronian to Whitneyan of northern Great Plains of North America, and earliest Oligocene of Asia.

Diagnosis—"Rostrum long and narrow; skull relatively narrower than in *Palaeocastor*; hypostria shallow; no canal piercing basioccipital at end of basispheno-basioccipital groove; bulla apparently kidney-shaped; dental formula 1.0.2.3, alveoli for incisor round…P3 represented by small alveoli; cheek teeth lower crowned than in *Palaeocastor*; P4 nearly square in outline; molars nearly rectangular in shape, elongate transversely; enamel borders of fossettes and flexi thicker than in *Palaeocastor*; fossettes and flexi wider than in *Palaeocastor*; mesostria and hypostria of equal or nearly equal length; two fossettes anterior to the mesostria in a late stage of wear." From Stirton (1935).

AGNOTOCASTOR CF. *A. PRAETEREADENS* Stirton, 1935

Table 7.1, Figure 7.3

Steneofiber nebrascensis Matthew, 1902

Holotype—AMNH 1428, nearly complete skull with LP4-M3 and RP4-M2, "*Protoceras* beds", Brule Formation, South Dakota.

Referred specimens from Rodent Hill —SMNH P2685.002 (RP4); P2706.026 (RM2); P2706.028 (Lp4).

Horizon at Rodent Hill—Both specimens collected in stratigraphically uncontrolled sampling.

Diagnosis—"Intermediate sized species (larger than *A. galushai*, smaller than *A. coloradensis*); occlusal pattern of cheek teeth less complex (fewer fossettes) than in other species; last premolars larger relative to molars than in other species; mandibular diastema shallow (less than 30% depth of mandible); rostrum not elongated as in *A. coloradensis*." Emended by Korth (2001b).

Description—The P4 is a mesodont tooth, with the crown enamel of the lingual side extended slightly below that of the buccal side. The tooth is wider than it is long, and rectangular in overall outline. The mesoflexus is the dominant feature of the tooth, extending from the buccal margin to more than midway across the tooth, terminating in a posteriorly directed curve that produces a J-shape. Two fossettes are present anteriorly to the mesoflexus, situated laterally to one another. The fossette closest to the buccal margin is nearly circular in outline; the second is situated roughly central in the anterior portion of the tooth, is ovate and open to the anterior margin via an anterobuccally directed flexus (paraflexus?). A short, ovate metafossette is present posteriorly to the mesoflexus, separated by a very small gap. The metafossette is connected to the posterobuccal margin, and nearly opens to form a metaflexus. The mesostria is a deep inflection, and continues to the base of the crown. A hypoflexus is present on the lingual side of the tooth that is approximately one third of the width of the tooth, anteroposteriorly wider than the mesoflexus, and oriented in an anterobuccal direction. The hypoflexus is almost directly in line with the "paraflexus". The hypostria on the lingual margin is narrower than the mesostria and does not extend to the base of the crown. The enamel between the fossettes and flexi of this tooth is relatively thick.

P2706.028 is a very unworn p4 with an anteroposteriorly elongate shape; the anterior portion has a slight transverse compression in comparison to the posterior end, and the crown enamel of the buccal margin is slightly deeper compared to that of the lingual margin. The hypoflexid does not extend deeply into the tooth, but is long, with an associated wide hypostriid that extends to just above the base of the crown. The mesoflexid is only barely open to the lingual margin, extends almost to the hypoflexid, and bends anterad midway along its length. The metafossettid is posterior to the mesoflexid, and almost opens to the posterolingual corner of the tooth. The metafossettid extends across the tooth to join with the mesoflexid as it curves anterad. There is a small, circular fossettid between the mesoflexid and metafossettid. On the lingual margin, next to the small fossettid, is a short ovate flexid open to the mesoflexid. On the anterior half of the tooth, the parafossettid is situated approximately centrally, extending about the same transverse length as the mesoflexid and metafossettid, is of an irregular shape, and is nearly open to the anterior margin. The parafossettid and mesoflexid are nearly joined together by an anterior extension of the mesoflexid. On the lingual margin, a short mesostriid is present that does not extend very far down the side of the tooth. The enamel on the buccal side of the tooth is relatively thick, whereas the enamel on the lingual side, around the more complex fossettids and flexids, becomes much thinner, pinching out posteriorly to the metafossettid, and along the anterobuccal margin.

Discussion—According to Xu (1996) and Storer (2002) the classification of castorids is primarily based on skull characteristics, and the individual teeth may not be assignable to genus or species. Unfortunately, dental material from Rodent Hill is almost always isolated, and as such cannot be definitely referred. These specimens are identified tentatively as being morphologically very similar to *Agnotocastor praetereadens* based on direct comparisons with SDSM 6420, SDSM 40167 and SDSM 40168 from South Dakota. In particular, the arrangement of fossettes on the P4 (P2685.002) and the morphology of the mesoflexid of the p4 (P2706.028) recall the descriptions of the South Dakota material given by Korth (2001b).

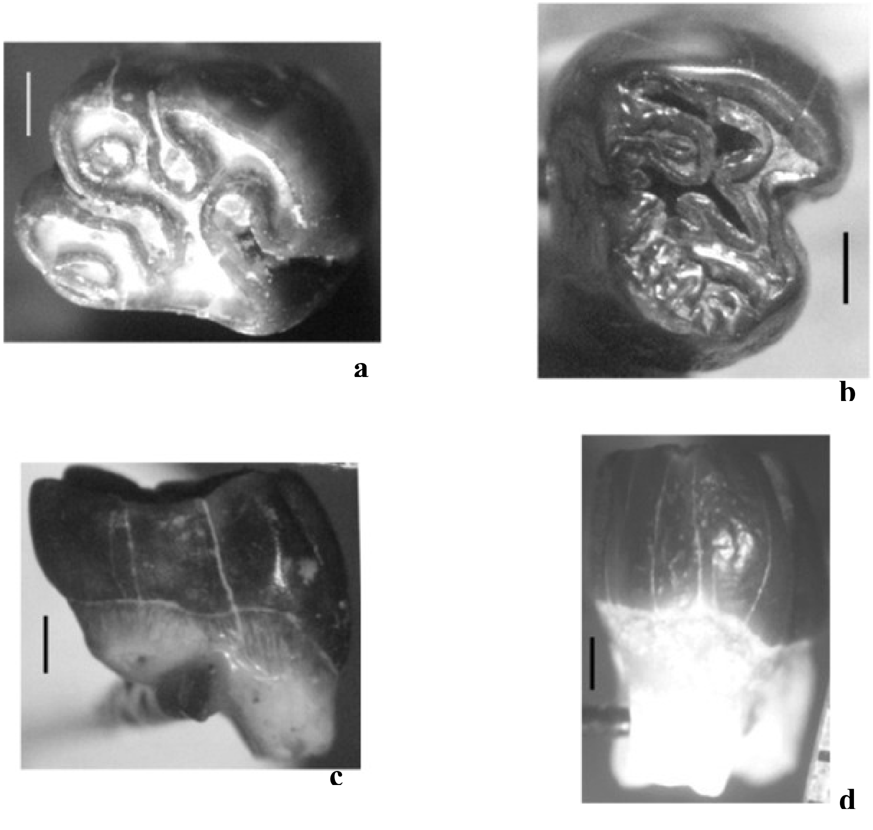


Figure 7.3 *Agnotocastor* cf. *A. praetereadens*: a. SMNH P2685.002 RP4; b. SMNH P2706.028 Lp4 c. SMNH P2685.002 anterior view; d. SMNH P2706.028 anterior view. Scale = 1mm, buccal of **a, c** to left of page; **b, d** to right.

OLIGOTHERIOMYS Korth, 1998a

Type species—*Oligotheriomys primus* Korth, 1998a

Referred species—?*O. senrudis* (Wood, 1945)

Age and distribution—Orellan of North Dakota, Whitneyan of Montana and Saskatchewan, possibly Hemingfordian of Montana and Wyoming.

Diagnosis—"Agnotocastorine beaver similar to *Anchitheriomys* and differing from other agnotocastorines in having a posterior maxillary notch rather than foramen, upper tooth rows diverge slightly (not as much as in castorines, palaeocastorines, and castoroidines), upper molars unilaterally hypsodont, occlusal pattern of cheek teeth more complex (more fossettes), and hypoflexus much shallower than on other agnotocastorines. Differs from *Anchitheriomys* in being much smaller (approximately half of all dental dimensions of *Anchitheriomys*), having cheek teeth lower crowned, P3 present (lost in *Anchitheriomys*), and lacking a deep mesoflexus on all upper molars (deep mesoflexus always present in *Anchitheriomys*)." From Korth (1998a).

? OLIGOTHERIOMYS SP.

Table 7.1, Figure 7.4

Referred specimen from Rodent Hill —SMNH P2838.003 (RM2?).

Horizon at Rodent Hill— Stratigraphic Unit VII.

Description—P2838.003 is somewhat rectangular, longer than wide, and low crowned. The tooth is relatively mesodont, and the lingual enamel is extended substantially more deeply than the buccal enamel. The hypoflexus does not extend very far into the tooth and is anterobuccally oriented. A hypostria is present on the lingual side that extends almost to the base of the crown, but does not reach it. From the buccal margin, the mesoflexus is the dominant feature, extending about half way across the width of the tooth as a narrow valley before curving sharply posterad. Only a very tiny

Figure 7.4 ?*Oligotheriomys* sp.: SMNH P2838.003 RM2?. Scale = 1mm, buccal to top of page.

mesostria is visible from the buccal edge of the mesoflexus. Two transverse fossettes (parafossettes?) are located anteriorly to the mesoflexus and extend the width of the occlusal surface. The longer of the two is marked by a slight expansion of the lingual portion of the fossette. Posteriorly to the mesoflexus is a transversely ovate fossette between the buccal margin and the posterior curve of the mesoflexus. An elongate fossette (metafossette?) extends across the width of the posterior margin. The center of the metafossette has an extension of the enamel that partially divides the fossette into a circular buccal portion and a more elongate lingual portion.

Discussion—This tooth most closely resembles the M2 of *Oligotheriomys primus* described by Korth (1998a), based on the buccally open mesoflexus with the sharp curve. Unfortunately, while being described, the tooth broke below the mesoflexus. The single transverse posterior fossette, on the other hand, resembles the M1 more, but the partial intrusion of the enamel could potentially be worn so that the single fossette would become two. When described by Korth (1998a) the complexity of the dentition of *Oligotheriomys* (and the related *Anchitheriomys*) was noted, and the majority of the fossettes were not identified using dental terms since they are not readily identifiable in the terminology first produced by Stirton (1935).

This specimen is unlikely to be *Oligotheriomys primus* due to the even more reduced number of anterior fossettes, and the smaller size. The unilateral hypsodonty (reduced in this specimen), lower crown height, shallow hypoflexus and higher degree of fossette complexity probably indicate that P2838.003 represents a different species within the genus. As with the *Agnotocastor* species described above, referring castorids based on isolated dentition alone is not generally feasible (Xu, 1996; Storer, 2002); however P2838.003 can probably be referred to *Oligotheriomys*.

? PALAEOCASTORINAE Martin, 1987

? PALAEOCASTORINAE, GEN. ET SP. INDET.

Table 7.1, Figure 7.5

Referred specimen from Rodent Hill—SMNH P2706.026 (Rm).

Horizon at Rodent Hill—Collected in stratigraphically uncontrolled sampling.

Description— The M2 (P2706.026) is a very worn tooth that is more hypsodont compared to the other Rodent Hill castorids, but still bears a root. The crown enamel appears deeper on the lingual margin, but this could be due to the intense wear on the buccal margin. The occlusal outline is somewhat ovate, with the tooth being greater in width than in length. No striae are visible on the sides of the tooth, possibly due to wear. The mesofossette is essentially straight, and oriented slightly posterolingually from the buccal margin. A single parafossette is located anteriorly to the mesofossette and they are roughly parallel to each other. The metafossette is transversely elongate, situated very close to the center of the posterior margin. The hypofossette extends from the lingual margin across the tooth anterolingually, nearly joining to the parafossette. The enamel surrounding the fossettes of this upper cheek tooth is raised slightly above the occlusal surface.

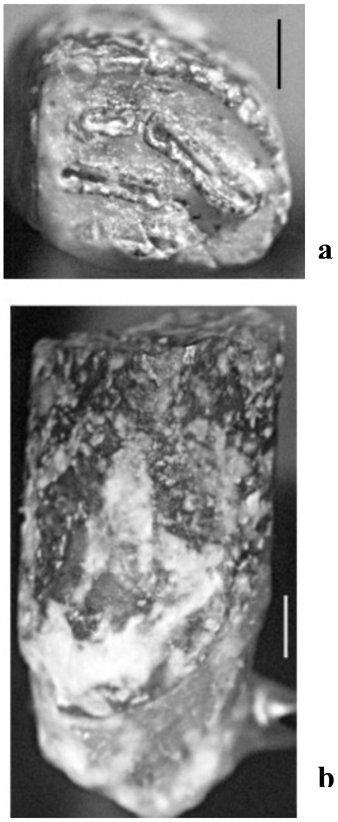


Figure 7.5 ? Palaeocastorinae, gen. et sp. indet.; a. SMNH P2706.026 Rm; b. SMNH P2706.026 posterior view. Scale = 1mm, buccal to right of page.

Discussion— The assignment of P2706.026 as a palaeocastorine beaver is based primarily on the tooth being more hypsodont than the other identifiable castorid teeth from Rodent Hill, and the simplified occlusal pattern (Xu, 1996; Korth and Emry, 1997; Korth, 2001b). The intense wear of the tooth has removed many features that might allow identification at least to genus, but this is certainly a distinct species from the other castorid material.

Table 7.1 Dental measurements of Rodent Hill castorids.

Taxon	Tooth position	Dimension	N	Mean
Agnotocastor cf. *A. praetereadens*	P4	AP	1	3.70
		TR	1	4.80
		LEH	1	3.50
		BEH	1	2.40
	p4	AP	1	4.20
		TRA	1	2.90
		TRP	1	3.80
		LEH	1	2.90
		BEH	1	3.90
? *Oligotheriomys* sp.	M2	AP	1	3.30
		TRA	1	2.40
		TRP	1	2.50
		LEH	1	3.00
		BEH	1	1.00
? Palaeocastorinae, gen. et sp. indet.	m	AP	1	3.00
		TR	1	3.80
		LEH	1	5.70
		BEH	1	3.70

CASTORIDAE, GEN. ET SP. INDET.

Referred specimens from Rodent Hill —SMNH P2452.130, P2521.044, P2521.046, P2521.360, P2834.002, P2834.011.

Horizon at Rodent Hill—Specimens P2834.002 and P2834.011 from Stratigraphic Unit I, all others collected in bulk sampling.

Descriptions—P2452.130 is the edge of a tooth with two isolated lakes present.

P2521.044 is a fragment from the center of a tooth. It appears to be a transverse flexid, divided into two lobes, one straight and one curved. Transversely opposite from the straight lobe is a transversely elongate fossettid.

P2521.046 is an indeterminate section of a tooth with several small fossettes/lakes on the surface (could potentially be a eutypomyid based on the large number of lakes).

P2521.360 is a fragment of a tooth with a single flexus/flexid with a fossette/fossettid present next to it.

P2834.002 is a fragment from the margin of a tooth. It is fairly high crowned and has an occlusal surface with several indeterminate lakes.

P2834.011 is from the lingual margin of a lower left molar. The hypoflexid is not extended deeply into tooth, and divides into two very short lobes at buccal end. A transversely elongate hypostylid is present posteriorly to the hypoflexid. A small, ovate metafossettid is located buccally to the hypostylid.

Discussion—All of these specimens are referable to the family Castoridae due to an identifiable feature, usually the presence of a fossette/fossettid or flexus/flexid. They are mentioned here briefly only to indicate that more fragmental castorid material has been recovered from the Rodent Hill Locality than identifiable castorid fossils. It appears that most of the castorid dentition that was recovered was quite worn in transport before deposition, due to the rounded appearance of the fracture surfaces on these specimens.

8. SUPERFAMILY GEOMYOIDEA

8.1 INTRODUCTION TO THE GEOMYOIDEA

The Superfamily Geomyoidea includes two extinct rodent families, the Florentiamyidae and Heliscomyidae, and two living families, the Heteromyidae and the Geomyidae.

This group of rodents has been restricted to North America since the appearance of the oldest known family, the Heliscomyidae, in the Uintan (Korth, 1994a). The ancestors of this family may have been within the family Sciuravidae (Korth, 1994a) but no definite ancestral lineage is known.

In all geomyoids the skulls are sciuromorphous, and the jaw is sciurognathous (Korth, 1994a).

The dental formula for all geomyoids is 1013/1013. The molars of these rodents (**Figures 8.1, 8.2)** are arranged in two transverse rows with two cusps each. The lingual margin of the uppers may bear one or more smaller stylar cusps. On the lowers, the stylar cusps occur on the buccal margin if they are present.

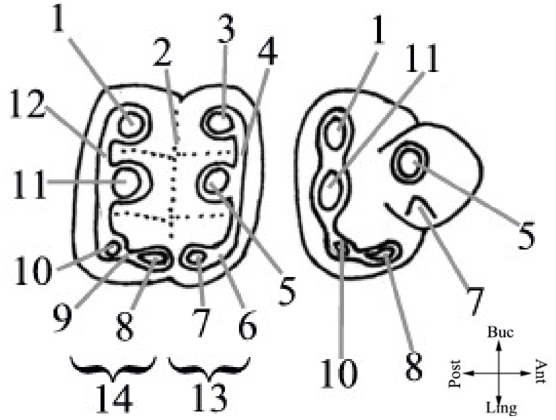


Figure 8.1 Generalized geomyoid upper cheek tooth morphology. RM1 (on left) and RP4 with major features identified. 1–metacone 2—transverse valley 3—paracone 4—anterior cingulum 5—protocone 6—lingual cingulum (anterior portion) 7—protostyle 8—entostyle 9—lingual cingulum (posterior portion) 10—hypostyle 11—hypocone 12—posterior cingulum 13—protoloph 14—metaloph

Drawn by the author, based on Korth (1994a). Terminology from Wood and Wilson (1936) and Korth (1994a)

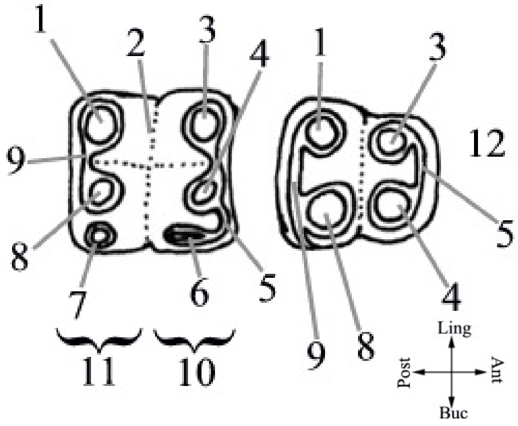


Figure 8.2 Generalized geomyoid lower cheek tooth morphology. Rm1 (on left) and Rp4, with major features identified. 1—entoconid 2—transverse valley 3—metaconid 4—protoconid 5—anterior cingulum 6—protostylid 7—hypostylid 8—hypoconid 9—posterior cingulum 10—metalophid 11—hypolophid

Drawn by the author, based on Korth (1994a). Terminology from Wood and Wilson (1936) and Korth (1994a).

8.2 FAMILY HELISCOMYIDAE

The Heliscomyidae is an extinct family of geomyoid rodents that are among the smallest rodents ever in North America (Korth, 1994a). The earliest heliscomyids have been identified from isolated teeth from Saskatchewan (Storer, 1987) and California (Kelly, 1992). Despite being the oldest geomyoid group, the Heliscomyidae is not considered directly ancestral to any later geomyoid family (Korth, 1994a). The peak diversity of the Heliscomyidae was in the Orellan and the family was extinct by the end of the Barstovian (Korth, 1994a). No species from this family have been described from a Whitneyan site but this was considered to be due to sampling errors rather than a real lack of heliscomyids at that time (Korth, 1994a). The description herein of three different heliscomyids supports the supposition that this family was present in the Whitneyan, but not yet described.

Heliscomyid dentition has the general geomyoid morphology, and is identifiable based on the very small size of the cheek teeth, the very brachydont crowns, and the stylar cusps that are much smaller than the cusps (Korth, 1994a).

8.2.1 Systematic Paleontology

GEOMYOIDEA Weber 1904

HELISCOMYIDAE Korth, Wahlert and Emry 1991

HELISCOMYS Cope 1873

Genotype—*Heliscomys vetus* Cope, 1873

Referred species—*H. gregoryi* Wood, 1933; *H. hatcheri* Wood, 1935a; *H. senex,* Wood, 1935; *H. woodi*, McGrew, 1941; *H. subtilis* (Lindsay, 1972); *H. mcgrewi* Korth, 1989; *H. ostranderi* Korth, Wahlert and Emry, 1991.

Age and distribution—Duchesnean of Saskatchewan; Chadronian of Wyoming, Montana, Nebraska and Saskatchewan; Orellan of the Great Plains and mountain states of the U.S.A, Saskatchewan?; Whitneyan of Saskatchewan and Montana; Arikareean of South Dakota; Hemingfordian of Saskatchewan; and Barstovian of California.

Diagnosis—Heliscomyid with p4 variably reduced (three- or four-cusped); entostyle present on M1; i1 and mandible slender, gracile. Korth *et al.* (1991) gave the most recent diagnosis for this genus.

Discussion—Although not previously described from the Whitneyan of the Cypress Hills Formation, *Heliscomys* specimens have previously been recovered from the Lac Pelletier fauna of Duchesnean age (Storer, 1988), the Calf Creek Local Fauna of Chadronian age (Storer, 1978) and the Topham local fauna of Hemingfordian age (Skwara, 1988).

HELISCOMYS (HELISCOMYS) Cope, 1873

Genotype—*Heliscomys vetus* Cope, 1873

Referred species—*Heliscomys (H.) senex,* Wood, 1935; *H. (H.) woodi*, McGrew, 1941; *H. (H.) mcgrewi* Korth, 1989.

Diagnosis—"Premolars reduced; dp4 simple, four-cusped, lacking any lophs; metaconid central when three-cusped on p4; width of P4 45-82 percent that of first molar, cusps other than hypocone often reduced or lost; lingual cingulum continuous on M1; protostyle lacking on upper molars." Diagnosis for subgenus from Korth, (1995).

HELISCOMYS (HELISCOMYS) VETUS Cope 1873

Table 8.1, Figure 8.3 a-c

Holotype—AMNH 5461, left mandible with p4-m1, Cedar Creek Member, White River Formation, Logan County, Colorado (Orellan).

Referred specimens from Rodent Hill—SMNH P2521.001, P2521.087 and P2521.090 (LM1); P2521.168, P2521.220, P2521.291, P2521.300 and P2834.019 (RM1); P2521.285 (LM2); P2834.013 (RM2); P2838.002 (Lm1); P2521.351 and P2836.001 (Rm1).

Horizon at Rodent Hill—P2834.013 and P2834.019 from Stratigraphic Unit I, P2836.001 from Stratigraphic Unit III and P2838.002 from Stratigraphic Unit VII. Other specimens collected by stratigraphically uncontrolled sampling.

Emended diagnosis—Approximately equal in size to *H. hatcheri*; premolars variable in morphology and relatively smaller than in *H. hatcheri*; continuous lingual cingulum and variable occurrence of entostyle on M1; no protostyle, or very reduced. Differs from *H. senex* by having an entostyle that may be rounded or ovate (always round in *H. senex*). The m1 of *H. vetus* may be distinguished from *H. hatcheri* by a

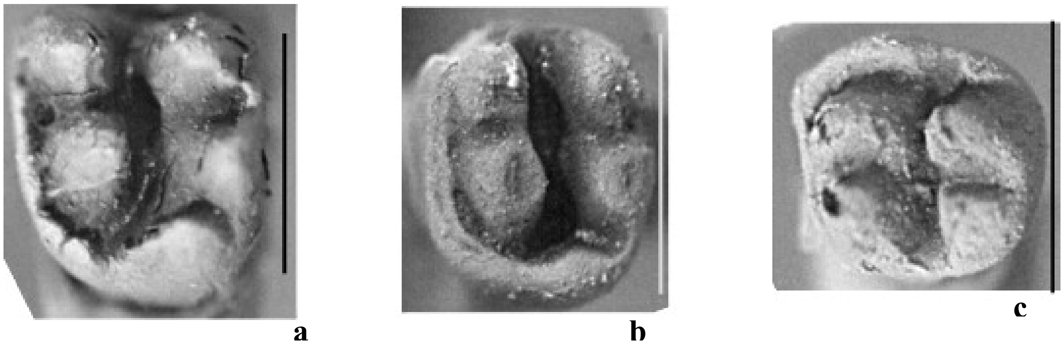


Figure 8.3 *Heliscomys (Heliscomys) vetus*: a. SMNH P2521.090 LM1; b. SMNH P2521.285 LM2; c. SMNH P2836.001 Rm1. Scale = 1mm, buccal to top.

weaker anterior cingulum and reduced stylid cusps. Korth's (1989c) diagnosis is emended here to include information about the lower molars.

Description—M1 has four cusps, with the protoloph offset buccally relative to the metaloph, giving the teeth an uneven appearance as the protoloph is not parallel to the metaloph. All of the cusps are circular, with the protocone being slightly larger. The paracone is set anterior to the protocone, accentuating the uneven appearance of M1; there is variation in how far forward the paracone is placed. An anterior cingulum is present that joins with a low lingual cingulum. On the continuous lingual cingulum there is no protostyle, but an entostyle is usually present that can vary from round to ovate. The entostyle is situated just posterior to the lingual end of transverse valley, and does not appear connected to the hypocone. The metaloph has a posterior cingulum between the metacone and hypocone that varies in width but is well defined.

M2 is nearly identical to M1 except that the protoloph and metaloph are parallel, although the protoloph may be slightly expanded buccally. In addition, the M2 appears to lack the posterior cingulum. In P2834.013, the cusps are worn very low, causing the entostyle to broaden anteriorly.

The m1 has an approximately square occlusal outline, and has four major cuspids and two smaller stylid cusps. The cuspids are arranged in the typical geomyoid pattern of two transverse rows. The metaconid and protoconid are generally quite close together but do not form a loph, and have an anterior cingulum extending almost the width of the tooth. The anterior cingulum is continuous with the anterior part of the buccal cingulum, which in turn terminates in a low, ovate protostylid. The protostylid is situated anteriorly to the transverse valley. The hypolophid is slightly compressed transversely compared to the metalophid, and the hypoconid and entoconid are further apart, joining at their bases with wear. A posterior cingulum is present only between the two major cuspids. The hypostylid is separated from the hypoconid.

Discussion—The material from Rodent Hill is assigned to *Heliscomys vetus* rather than *H. senex* based on direct comparisons with referred material; however the species are diagnosed based on complete tooth rows, primarily using P4 and p4, meaning that isolated dentition is very difficult to tell apart. Korth (1989c) synonymised these two species based on their apparent similarities, but later reversed this decision (Korth, 1995) after finding a skull and associated mandible of *H. senex*. There is, however, no doubt that the Rodent Hill specimens belong to one of these species, and that they are morphologically most similar to *H. vetus*, particularly in the variable presence and shape of the entostyle on M1. *Heliscomys vetus* also appears to be more variable in size (Galbreath, 1953) and this variability is evident in the Rodent Hill specimens. The Rodent Hill specimens identified as *Heliscomys vetus* are also distinguishable from the similar sized *H. hatcheri* and *H. gregoryi* by the lack of the protostyle and the continuous lingual cingulum.

Four specimens (P2521.090, P2521.168, P2521.220 and P2521.291) are larger anteroposteriorly than any specimen of this species previously described. This difference is interpreted as a minor increase in size (no more than 10% larger) within the species over time, so that some of the Whitneyan individuals were larger than some Orellan individuals. Given the small number of specimens present at Rodent Hill, the size difference is not considered sufficient to warrant a new species for only four individual teeth.

Table 8.1 Dental measurements of *Heliscomys (Heliscomys) vetus*.

Tooth position	Dimension	N	Mean	OR	SD	CV
M1	AP	7	0.95	0.83-1.03	0.08	8.59
	TR	7	1.10	1.03-1.15	0.05	4.91
M2	AP	2	0.87	0.86-0.88		
	TR	2	1.08	1.04-1.13		
m1	AP	3	0.80	0.70-0.90		
	TRA	3	0.88	0.86-0.90		
	TRP	3	0.82	0.77-0.89		

HELISCOMYS (SYPHYRIOMYS) KORTH, 1995

Genotype—*Heliscomys hatcheri* Wood, 1933

Referred species— *Heliscomys (S.) gregoryi* Wood, 1933; *H. (S.) subtilis* (Lindsay, 1972); *H. (S.) ostranderi* Korth, Wahlert and Emry, 1991.

Diagnosis—"P4 four-cusped with width 77-95 percent that of M1; dp4 with accessory cuspules and anteroposterior lophs; metaconid non-central on three-cusped p4; lingual cingulum on M1-M2 broken by valley, protostyle present on M1-M2 on all but the most primitive species" Diagnosis from Korth, (1991).

HELISCOMYS (SYPHYRIOMYS) HATCHERI Wood 1935a

Table 8.2, Figure 8.4 a-c

Holotype—USNM 6635, partial mandible with m1-m2, Cottonwood Creek, Orella Member, Brule Formation, Sioux County, Nebraska (Orellan).

Referred specimens from Rodent Hill—SMNH P2521.286, maxilla fragment with LM1-2; P2521.386 and P2835.002 (RM1); P2521.368 (LM2); P2452.114, P2452.117, P2521.034, P2521.147, P2521.190, P2521.263, P2521.391 and P2834.006 (Lm1); P2521.149, P2521.152, P2521.161, P2521.256, P2521.317, P2521.352, P2521.375, P2835.005 and P2836.005 (Rm1); P2521.295 (Lm2); P2521.320, P2521.344 and P2521.374 (Rm2).

Horizon at Rodent Hill—P2834.006 from Stratigraphic Unit I, P2835.002 and P2835.005 from Stratigraphic Unit II and P2836.005 from Stratigraphic Unit V. Other specimens collected by stratigraphically uncontrolled sampling.

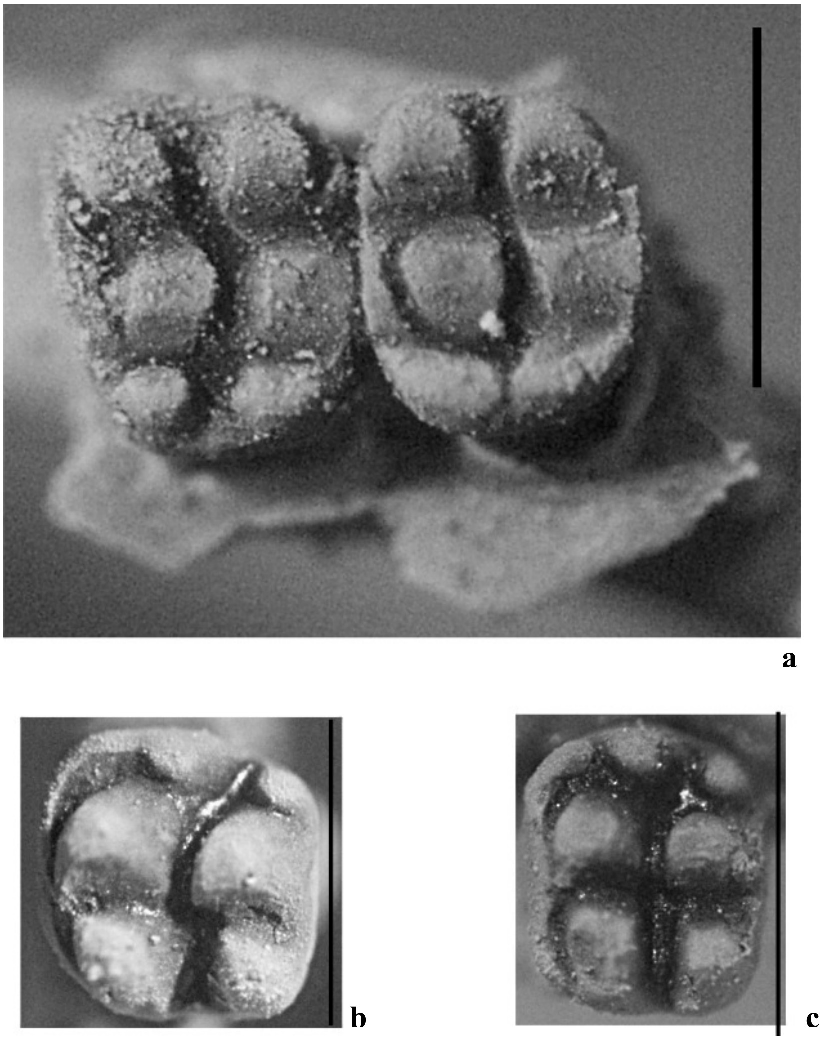


Figure 8.4 *Heliscomys (Syphyriomys) hatcheri*: a. SMNH P2521.286 L maxilla fragment M1&M2; b. SMNH P2521.161 Rm1; c. SMNH P2521.320 Rm2. Scale = 1mm, buccal to top of page.

Emended Diagnosis—Equal in size to *H. vetus*; premolars variable in morphology and relatively larger than in *H. vetus*; upper molars with distinct entostyle and protostyle and discontinuous lingual cingulum. The m1 of *H. hatcheri* may be distinguished from *H. vetus* by a stronger anterior cingulum and better-developed stylid cusps. Originally diagnosed by Wood (1935a), emended by Korth (1989c). The diagnosis is emended here by incorporating information about the lower molars.

Description—M1 and M2 are both sextituberculate teeth arranged in two transverse rows, with four larger main cusps and two smaller style cusps on the lingual margin. M1 is slightly larger anteroposteriorly than M2, with a more pronounced interruption in the lingual cingulum, increasing the gap between the protostyle and entostyle relative to M2. With wear, the interruption of the cingulum can become less pronounced, existing as a tiny notch, but the style cusps remain relatively pronounced. On the M1, a slight buccal offset of the protoloph relative to the metaloph gives the tooth an uneven appearance; this offset is not apparent in M2. An anterior cingulum that extends most of the width of the tooth is present on both M1 and M2, whereas a posterior cingulum is present only on M1

The m1 specimens are variably squared in outline, with four large major cuspids and two smaller stylid cuspids, a protostylid and hypostylid. An anterior cingulum is present across the width of the tooth and may expand anterad causing the buccal end of the anterior cingulum to be wider than the lingual end. The anterior cingulum extends around to the buccal edge to join the buccal cingulum that terminates at the protostylid. The protostylid does not extend past the transverse valley. On the hypolophid, a variable posterior cingulum may extend the width of the tooth, or may exist only as a reduced shelf between the hypoconid and entoconid (this reduction could also be due to wear of the tooth). The hypostylid is placed on the buccal margin, well posterior to the anterior margin of the hypoconid.

The m2 is similar to the m1, but anteroposteriorly shorter, giving a slightly rectangular outline. As with the m1, the tooth is arranged in two transverse rows of two larger main cuspids and a smaller stylid cusp. There is the same anterior cingulum that extends around the anterobuccal corner to the protostylid, but there is no recognizable posterior cingulum.

Table 8.2 Dental measurements of *Heliscomys (Syphyriomys) hatcheri*.

Tooth position	Dimension	N	Mean	OR	SD	CV
M1	AP	3	0.85	0.82-0.88		
	TR	3	0.99	0.96-1.00		
M2	AP	2	0.79	0.78-0.80		
	TR	2	1.00	0.98-1.03		
m1	AP	16	0.87	0.85-1.00	0.23	4.66
	TRA	17	0.90	0.82-1.00	0.05	5.48
	TRP	17	0.87	0.81-0.96	0.05	5.65
m2	AP	4	0.84	0.83-0.88	0.02	2.79
	TRA	4	0.90	0.88-0.92	0.02	2.36
	TRP	4	0.89	0.85-1.00	0.07	8.03

Discussion—As well as being approximately equal in size, these specimens are morphologically very similar to previously described *Heliscomys hatcheri* specimens. Some specimens, most notably P2835.005, are larger than any other referred *H. hatcheri* specimens; however, all Rodent Hill specimens are within 10% of the dimensions of comparable specimens. Only P2835.005 is larger by 15% transversely, being closer in size to *H. gregoryi* (see below), but it is included with *H. hatcheri* for morphological reasons as representing a slightly larger individual.

The Rodent Hill specimens are representative of the subgenus *H. (Syphyriomys)* erected by Korth (1995) to distinguish the *Heliscomys* species with interrupted lingual cingula and relatively larger P4 (although no upper premolars were recovered at this locality) from those with continuous lingual cingula and relatively small P4. This distinction serves to separate the *H. hatcheri* specimens from those of *H. (Heliscomys)* *vetus* and *H. (H.) senex*. Unfortunately, no distinction between the subgenera was made at the time based on lower molars, and it remains to be seen if the distinctions provided in the emended diagnoses of this species and *H. vetus* (below) are applicable to the subgenera as well.

It is necessary to distinguish the Rodent Hill specimens from a similarly sized *H. (Syphyriomys)* species, *H. (S.) gregoryi*. Korth (1989) gives four distinguishing characteristics to differentiate these two species. *Heliscomys (S.) hatcheri* is distinguished from *H. (S.) gregoryi* by a posterior cingulum on M1, deeper separation of protostyle and entostyle on M1, poor separation of protostyle and entostyle on M2, and less reduction of M3. As indicated by the posterior cingulum and the wide separation of the entostyle and protostyle of M1, and the poor separation of the entostyle from the protostyle on M2 as seen in the Rodent Hill specimens, the small *H. (Syphyriomys)* specimens should be regarded as *Heliscomys (S.) hatcheri*.

HELISCOMYS (SYPHYRIOMYS) SP. INDET.

Table 8.3, Figure 8.5

Referred specimens from Rodent Hill—SMNH P2521.381 (LM1); P2452.112 and P2521.369 (LM2).

Horizon at Rodent Hill—Collected by stratigraphically uncontrolled sampling.

Description—M1 has four cusps, with the protoloph extended buccally relative to the metaloph, giving the tooth an uneven appearance. All of the cusps are circular and distinct, with the protocone being the largest. The paracone is offset slightly anteriorly to the protocone, giving an uneven appearance to the tooth. An anterior cingulum extends from the anterior margin of the paracone on the buccal end and curves around the anterolingual corner on the lingual end. The anterior cingulum terminates in a protostyle that is present as a small swelling. The lingual cingulum is not continuous, but instead is deeply divided at the lingual end of the deep central transverse valley. Across this gap from the protostyle is a very well developed entostyle that extends to partially block the central transverse valley. The entostyle is separated from the hypocone by a narrow gap. The cusps of the metaloph are spaced widely apart and distinct, with a well-developed, deep posterior cingulum posterad to the metacone that extends to the buccal side of the hypocone.

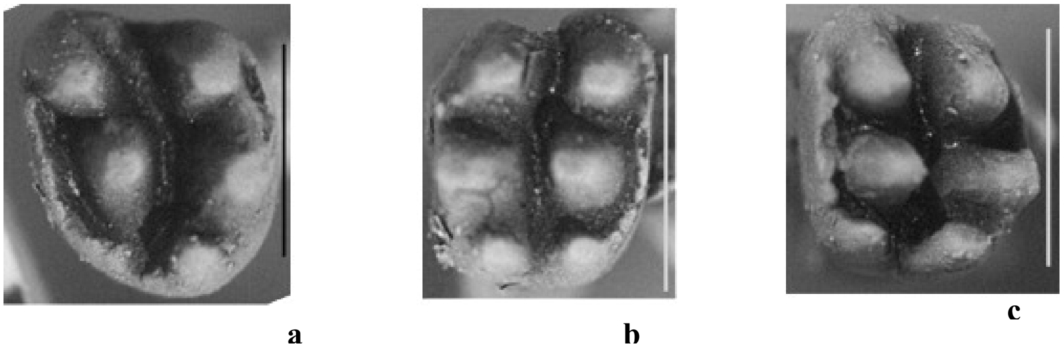


Figure 8.5 *Heliscomys (Syphyriomys)* sp. indet.: a. SMNH P2521.381 LM1; b. SMNH P2452.112 LM2; c. SMNH P2521.369 RM2. Scale = 1mm, buccal to top of page.

The M2 is smaller than M1 with better-developed stylar cusps, giving a more strongly sextituberculate occlusal pattern. The cusps of the protoloph are separated as in M1, and the paracone is situated slightly buccal and anterior to the protocone. An anterior cingulum appears to terminate at the lingual margin of the tooth and continues into the well-developed protostyle. There is a gap that is almost the width of the transverse valley between the protostyle and entostyle. The lingual cingulum is dominated entirely by the stylar cusps. The hypocone and metacone are well divided as in the M1, and are joined by a posterior cingulum.

Table 8.3 Dental measurements of *Heliscomys (Syphyriomys)* sp. indet.

Tooth position	Dimension	N	Mean	OR
M1	AP	1	1.15	0.82-0.88
	TR	1	1.20	0.96-1.00
M2	AP	2	0.94	0.93-0.95
	TR	2	1.09	1.09-1.10

Discussion—These specimens are placed within the subgenus *Syphyriomys* due to the interruption of the lingual cingulum of the M1 and the development of both a protostyle and entostyle (Korth, 1995). The uppers share the narrow gap between the protostyle and entostyle on M1 and the deep divide on the cingulum of M2, characteristic of *Heliscomys gregoryi* (Korth, 1989c). However, there is a well-developed posterior cingulum on the M1 that is more characteristic of *H. hatcheri*.

The heliscomyid specimens described above are distinguishable by their size from any known Orellan or Arikareean species of *Heliscomys*, or any other heliscomyid. The teeth are larger than those of *H. hatcheri* or *H. vetus* by as much as 45% (depending on tooth position and compared specimen). Only the Orellan *Heliscomys mcgrewi*, the largest species in the family, is similar in size. On average, *Heliscomys mcgrewi* is larger by 6% anteroposteriorly and 18% transversely, based on dimensions given by Korth (1989c). Most specimens of *H. mcgrewi* are larger than the Rodent Hill specimens, except for one M1 that is 4% smaller. The Rodent Hill specimens cannot be

H. mcgrewi due to the absence of the continuous lingual cingulum that is present in *H. mcgrewi*.

The size and morphology of these specimens probably indicates a distinct species, but the material available is very limited and would not make good holotypic material. It is hoped that similar finds in a locale that produces complete associated upper and lower dentitions may help to characterize this taxon better.

8.3 FAMILY FLORENTIAMYIDAE

This extinct family of geomyoid rodents first arose in the Orellan and has only been found from the Great Plains of North America (Korth, 1994a). The family was extinct by the Barstovian. The diversity of the Florentiamyidae peaked in the Arikareean (Korth, 1994a).

The upper cheek teeth of the Florentiamyidae are brachydont and bear an anteroposteriorly elongate entostyle on the lingual cingulum that blocks the transverse valley (Wahlert, 1983). The lower molars have well-developed stylar cusps that are not as large as the main cusps (Korth, 1994a).

8.3.1 Systematic Paleontology

FLORENTIAMYIDAE Wood 1936

KIRKOMYS Wahlert 1984

Genotype—*Kirkomys milleri* Wahlert, 1984

Referred species—*K. schlaikjeri* (Black, 1961).

Age and distribution—Orellan of South Dakota; Whitneyan of Nebraska and Saskatchewan; early Arikareean of Wyoming.

Emended diagnosis—Upper molars of *Kirkomys* are smaller than those of *Florentiamys* or *Sanctimus* and larger than those of *Ecclesimus*; anteroposteriorly elongate entostyle characteristic of florentiamyids present on the continuous lingual cingula of M1 and M2. P4 with protocone and supporting root on the anterior part of the tooth, and paracone and parastyle absent. Incisive foramina very short, approximately 12% of diastemal length. Posterior palatine, dorsal palatine, sphenopalatine and optic foramina and anterior-alar fissure farther anterior than in *Florentiamys* and *Sanctimus*. No marginal flanges on frontal bones over orbits. Diagnosis from Wahlert (1984).

Discussion—The diagnosis has been emended to compare *Kirkomys* with *Ecclesimus*.

KIRKOMYS MILLERI Wahlert 1984

Table 8.4, Figure 8.6

Holotype—F:AM 105337, snout, palate, orbit with LI1-LM3 and RP4-RM3, Brule Formation, Nebraska.

Referred specimens from Rodent Hill—SMNH P2521.172, P2521.230 and P2834.016 (LM1); P2452.148, P2521.354 and P2521.373 (RM1); P2521.193 (LM1 orM2); P2521.088 and P2521.089 (RM2); P2521.274 (LM3); P2521.216 and P2521.228 (RM3).

Horizon at Rodent Hill—P2834.016 from Stratigraphic Unit I. Other specimens collected in stratigraphically uncontrolled sampling.

Diagnosis—Cheek teeth proportionally larger than in *K. schlaikjeri*, having deep separation between protocone and entostyle; posterior cingulum absent on P4; anterior cingulum on molars narrow; maximum curvature of edge of maxilla into zygoma anterior to P4. From Wahlert (1984).

Description—The M1 and M2 are low crowned with four circular main cusps and a lingual cingulum bearing a smaller, lower entostyle that blocks the transverse valley. The entostyle is better developed on the M1 than on the M2. On most specimens that clearly display the entostyle it is low and anteroposteriorly elongate, while on one M1, P2521.172, the entostyle is slightly higher. This tooth is interpreted as an unworn tooth of *Kirkomys* due to the high, relatively pointed nature of all of the cusps. The protoloph and metaloph of the M1 and M2 each bear two closely appressed cusps, and the lophs are parallel to subparallel. On some M1 specimens (P2521.354, P2834.016) there is a slight offset buccally of the protoloph so that the paracone and protocone are situated slightly buccad to the metacone and hypocone, respectively. This apparent offset is not present on the M2 specimens; instead, the posterior margin of the metaloph of the M2 specimens is very slightly convex compared to the straight metaloph of the M1 specimens. A distinct anterior cingulum, present on all M1 and M2 specimens, connects with the lingual cingulum; this latter cingulum is widely separated from the protocone. In the M2 P2521.089 there is an accessory crest that extends anterad from the protocone to the anterior cingulum. A low, narrow posterior cingulum is present on most M1 specimens, although the exact position varies widely, either being situated between the hypocone and metacone, extending from the buccal edge of the hypocone to terminate posteriorly to the metacone, or being situated posteriorly to the metacone only. The M2 specimens do not show any posterior cingulum.

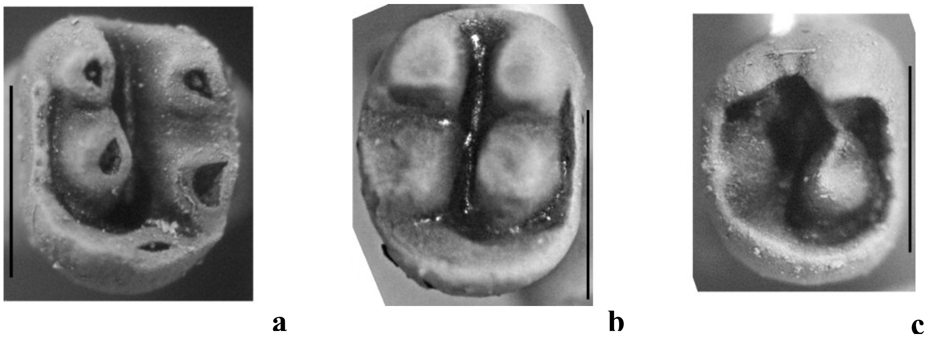


Figure 8.6 *Kirkomys milleri*: a. SMNH P2834.016 LM1; b. SMNH P2521.088 RM2; c. SMNH P2521.216 LM3. Scale = 1mm, buccal to top of page.

Description—The M1 and M2 are low crowned with four circular main cusps and a lingual cingulum bearing a smaller, lower entostyle that blocks the transverse valley. The entostyle is better developed on the M1 than on the M2. On most specimens that clearly display the entostyle it is low and anteroposteriorly elongate, while on one M1, P2521.172, the entostyle is slightly higher. This tooth is interpreted as an unworn tooth of *Kirkomys* due to the high, relatively pointed nature of all of the cusps. The protoloph and metaloph of the M1 and M2 each bear two closely appressed cusps, and the lophs are parallel to subparallel. On some M1 specimens (P2521.354, P2834.016) there is a slight offset buccally of the protoloph so that the paracone and protocone are situated slightly buccad to the metacone and hypocone, respectively. This apparent offset is not present on the M2 specimens; instead, the posterior margin of the metaloph of the M2 specimens is very slightly convex compared to the straight metaloph of the M1 specimens. A distinct anterior cingulum, present on all M1 and M2 specimens, connects with the lingual cingulum; this latter cingulum is widely separated from the protocone. In the M2 P2521.089 there is an accessory crest that extends anterad from the protocone to the anterior cingulum. A low, narrow posterior cingulum is present on most M1 specimens, although the exact position varies widely, either being situated between the hypocone and metacone, extending from the buccal edge of the hypocone to terminate posteriorly to the metacone, or being situated posteriorly to the metacone only. The M2 specimens do not show any posterior cingulum.

The anterior half of M3 is slightly narrower but similar to the other molars, bearing a narrow anterior cingulum separated from a protoloph with well-developed protocone and paracone. The metaloph is buccolingually shortened, with a poorly developed cuspule where the hypocone would be expected, and a low metacone. There is no distinct posterior cingulum. A minor expansion on the lingual cingulum indicates the presence of any entostyle blocking the transverse valley. The lingual cingulum, as on M1 and M2, is a continuation of the anterior cingulum, and is well separated from the protocone. With wear, the metaloph appears to join with the buccal margin to form a continuous crest that is lower than the protoloph; in the extreme wear indicated by P2521.274, this posterobuccal crest can be worn down to approximately the same height as the central valley.

Table 8.4 Dental measurements of *Kirkomys milleri*.

Tooth position	Dimension	N	Mean	OR	SD	CV
M1	AP	6	1.21	1.15-1.28	0.05	3.85
	TR	6	1.50	1.38-1.58	0.09	5.92
M1-2	AP	1	1.15			
	TR	1	1.23			
M2	AP	2	1.14	1.13-1.15		
	TR	2	1.52	1.50-1.53		
M3	AP	3	1.07	1.03-1.10		
	TR	3	1.26	1.08-1.35		

Discussion—All specimens referred to *Kirkomys milleri* are upper dentition. There is the possibility that *K. milleri* is synonymous with *Proheteromys nebraskensis.* This situation is described in more detail in the *P. nebraskensis* discussion below.

The Rodent Hill specimens are considered florentiamyids because they share the typical florentiamyid molar morphology of four large main cusps in two transverse rows and a lingual cingulum containing an anteroposteriorly elongate entostyle (Wahlert, 1983). The Cypress Hills material is referred to *K. milleri* due to the diagnostic narrow anterior cingulum and deep separation between the protocone and entostyle as seen in the holotype and only previously known specimen, F:AM 105337 (Wahlert, 1984). The Rodent Hill specimens are generally larger than the holotype (maximum 7% difference anteroposteriorly, and 9% difference buccolingually in unbroken specimens) but this is considered to be a reasonable amount of variation within the species.

ECCLESIMUS Korth, 1989c

Genotype and only species—*Ecclesimus tenuiceps* (Galbreath, 1948)

Age and distribution—Orellan of Colorado and Nebraska, Whitneyan of Saskatchewan

Diagnosis—Smaller than *Kirkomys* and later florentiamyids; paracone variably present on P4; M3 smaller relative to M2 than in other genera. From Korth (1989c).

?*ECCLESIMUS* SP.

Table 8.5, Figure 8.7

Referred specimens from Rodent Hill—SMNH P2521.395 (LP4); P2521.087 (LM1); P2521.400 and P2838.004 (RM2); P2452.113 and P2521.086 (LM2); P2521.040 (LM3); P2836.002 (Rm1); P2521.170 and P2834.018 (Lm1); P2452.118, P2521.203 and P2834.015 (Lm2).

Horizon at Rodent Hill—P2834.004, P2934.015 and P2834.018 collected from Unit I, P2836.002 collected from Unit V. All other specimens collected by stratigraphically uncontrolled sampling.

Description—The P4 is four cusped, with a protoloph that bears a large central protocone and a much smaller paracone that is slightly anterior. The metaloph has two major cusps, a hypocone and metacone, which are equal in size to the protocone, and a smaller hypostyle that is separated by a gap from the hypocone. The hypostyle does not extend beyond the anterior margin of the metaloph. There is a posterior cingulum between the metacone and hypocone that does not extend beyond the cusps, and no anterior cingulum is apparent.

M1 has four major cusps in two subparallel transverse rows, each with a small transversely compressed stylar cusp. The protocone and paracone are distinct cusps and are joined by only a very narrow crest. The paracone is situated slightly anteriorly to the protocone, giving the subparallel appearance to the lophs. There is a wide anterior cingulum that curves around the anterolingual corner to join with the lingual cingulum. There is a wide gap between the protocone and the lingual cingulum. The lingual cingulum is interrupted by a very shallow depression between the protostyle and the entostyle. The lingual end of the central transverse valley is blocked by the long, very narrow entostyle. The hypocone and metacone on the metaloph are also set widely apart, and may be connected posteriorly by a distinct posterior cingulum.

The M2 has four bulbous cusps, with the anterior cusps being more pronounced than the posterior cusps. A valley that is not quite as deep as the central transverse valley separates the anterior cusps. A narrow anterior cingulum that originates from the anterolingual corner of the paracone extends around the lingual margin to join with the lingual cingulum. There is a small protostyle present at the anterolingual corner of the tooth along the lingual cingulum. The lingual cingulum is separated widely from the protocone and bears an anteroposteriorly elongate entostyle that blocks the lingual end

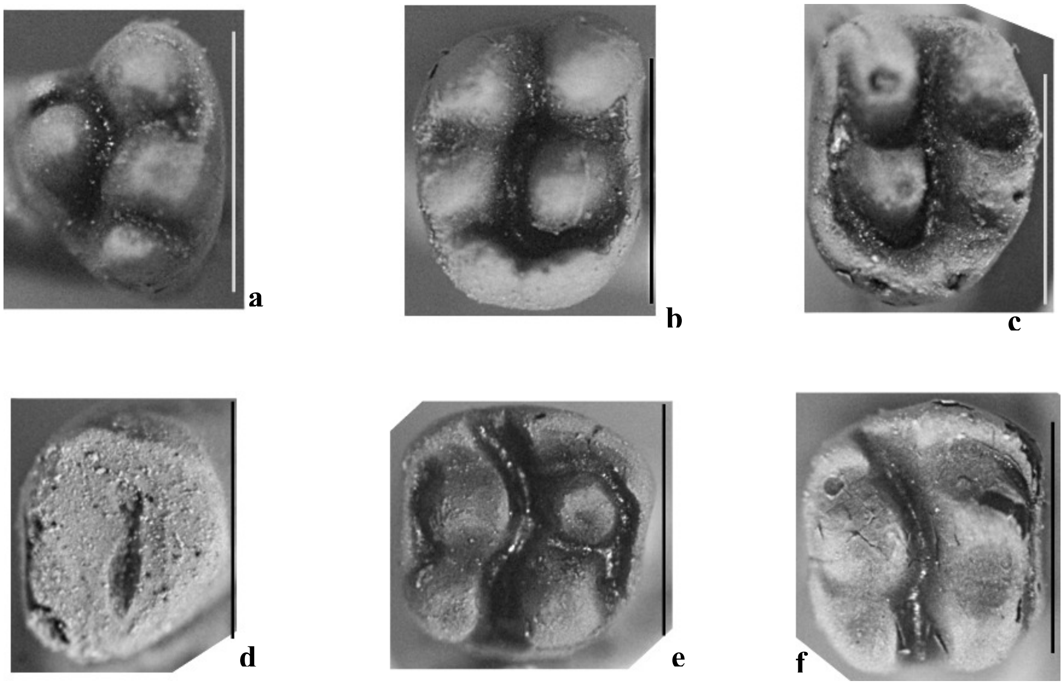


Figure 8.7 ? *Ecclesimus* sp.: a. SMNH P2521.395 LP4; b. SMNH P2521.400 RM1; c. SMNH P2452.113 RM2; d. SMNH P2521.040 LM3; e. SMNH P2834.018 Lm1; f. SMNH P2521.203 Lm2. Scale = 1mm, buccal to top of page.

of the transverse valley. The lingual cingulum continues around to the posterior margin of the tooth, where it forms a ridge with the metaloph, and terminates at the posterolingual corner of the metacone. The hypocone and metacone are both well developed and are similar in size. Both posterior cusps are about equal in height to the protocone, and are connected by the posterior ridge. At the buccal margin of the tooth, a wide transverse valley separates the protoloph and metaloph.

Table 8.5 Dental measurements of ? *Ecclesimus* sp.

Tooth position	Dimension	N	Mean	OR
P4	AP	1	0.85	
	TR	1	1.08	
M1	AP	2	0.92	0.90-0.93
	TR	2	1.20	1.15-1.25
M2	AP	3	0.96	0.95-0.98
	TR	3	1.19	1.15-1.23
M3	AP	1	0.78	
	TR	1	1.08	
m1	AP	3	1.17	1.10-1.25
	TRA	3	1.09	1.08-1.10
	TRP	3	1.06	1.05-1.08
m2	AP	3	1.04	0.98-1.10
	TRA	3	1.13	1.10-1.15
	TRP	3	1.06	1.03-1.10

The only M3 is worn such that no cusps or features are readily visible. It is much smaller than the M2. The protoloph is transversely wider than the metaloph and extends further buccally. The protoloph appears to connect to the metaloph via the lingual cingulum and with wear has joined at the buccal margin, creating a central pit on the tooth.

The m1 has four major cuspids arranged in two transverse rows, and very small, poorly developed stylid cusps. The cuspids of the metalophid are situated close together but are distinct and do not appear to form a single lophid. There is an anterior cingulum that extends for the entire length of the metalophid, and curves around to join with the buccal cingulum. The anterior cingulum varies in its length, and in one specimen (P2836.002) is expanded anterobuccally compared to the anterolingual margin. The buccal cingulum is interrupted at the transverse valley. The protostylid is poorly developed, appearing as little more than a slightly higher widening on the cingulum, and is situated slightly posteriorly to the anterior margin of the transverse valley. The cuspids of the hypolophid are set further apart and are about the same size as the cuspids of the metalophid. The hypoconid extends anterad into the transverse valley. There is a distinct posterior cingulum across the posterior width of the tooth, which curves around on the buccal margin to join the buccal cingulum and terminates at the hypostylid. The hypostylid is better developed than the protostylid, circular in appearance, and definitely higher than the cingulum.

The m2 is smaller than the m1 and appears anteroposteriorly shorter. The protoconid is larger than the metaconid, and the two are more closely appressed than in m1, forming a more loph-like structure as the tooth wears. There is a narrow, straight anterior cingulum that does not deviate in width, unlike on m1. The anterior cingulum is continuous with the buccal cingulum, terminating in a well-developed ovate protostylid that is lower than the metalophid. The protostylid does not extend posteriorly beyond the anterior margin of the transverse valley. On the hypolophid the hypoconid is the larger cusp, expanding anteriorly into the transverse valley. The hypoconid may begin to join to the metalophid with wear. The hypoconid and entoconid join to form a distinct loph with wear. A variable posterior cingulum extends from about midway along the width of the tooth and terminates at the hypostylid. The hypostylid is circular and smaller than the protostylid, and with wear becomes joined with the hypolophid.

Discussion—These teeth are referred to the Florentiamyidae based on the characteristic entostyle blocking the central transverse valley (Wahlert, 1983). They are questionably referred to *Ecclesimus* based on size as they are very similar in size and proportions to that genus (7% larger anteroposteriorly, 16% larger transversely) and have an M3 that is much smaller than M2 (Korth, 1989c). They are also distinctly smaller than the *Kirkomys* specimens recovered from the site.

The lowers have been referred to this taxon more for convenience than any other reason. They are larger than those referred to the *Heliscomys* species from Rodent Hill, but smaller than the *Proheteromys* specimens. Since no lowers have been described for *Ecclesimus* these would be the first ones identified, but the assignment of these teeth is tentative.

8.4 FAMILY HETEROMYIDAE

The family Heteromyidae first appeared in the Whitneyan of North America (Korth, 1994a) and is extant in North America as the modern kangaroo rats and pocket mice. The diversity of the family was highest during the Barstovian

8.4.1 Systematic Paleontology

HETEROMYIDAE Gray 1868

PROHETEROMYS Wood 1932

Genotype—*Proheteromys floridanus* Wood, 1932

Referred species—The species in this list are based on Korth (1997). *P. parvus* (Troxell, 1923); *P. magnus* Wood, 1932; *P. matthewi* Wood, 1935a; *P. thorpei* Wood, 1935; *P. nebraskensis* Wood, 1937; *P. fedti* Macdonald, 1963; *P. gremmelsi* Macdonald, 1963; *P. sulculus* Wilson, 1960; *P. maximus* James, 1963; *P. cejanus* Gawne, 1975.

Age and distribution—Orellan of South Dakota; Whitneyan of Nebraska, South Dakota, Saskatchewan; Arikareean of Nebraska, South Dakota, Colorado?;

Hemingfordian of Florida, South Dakota, New Mexico, Saskatchewan and Colorado?; and Barstovian of California.

, but since the Arikareean there have always been several species (Korth, 1994a).

The cheek teeth of heteromyids vary from brachydont in the earlier species to hypsodont in later taxa (Korth, 1994a). All of the molars of heteromyids have two transverse lophs with three cusps each (Korth, 1994a). The stylar cusps are almost the size of the principal cusps (Korth ,1994a).

Diagnosis—Cheek teeth bilophodont and in about the same stage of development as in *Mookomys*, and likewise based upon a primarily sextitubercular pattern; upper incisors asuclate; p4 quadritubercular; posterior cingula on lower and anterior cingula on upper teeth. From Wood (1932).

PROHETEROMYS NEBRASKENSIS Wood 1937

Table 8.6, Figure 8.8

Holotype—MCZ 5051, left mandible with p4-m3, Morrill County, Nebraska.

Referred specimens from Rodent Hill—SMNH P2521.210 (Lp4); P2521.092, P2521.219 and P2521.301 (Lm1); P2521.025, P2521.211, P2521.264, P2521.275, P2834.012 and P2838.005 (Rm1); P2452.115, P2452.119 and P2521.081 (Lm2); P2521.054, P2521.197, P2521.306 and P2521.353 (Lm3) and P2521.283 (Rm3).

Horizon at Rodent Hill—P2834.012 from Stratigraphic Unit I, and P2838.005 from Stratigraphic Unit VII. Other specimens collected by stratigraphically uncontrolled sampling.

Diagnosis—Intermediate in size between *P. floridanus* and *P. parvus*; teeth are proportionately long antero-posteriorly; posterior cingula are weak; protostylid of molars separate from cingulum when unworn, and is far to the rear; protoconid and metaconid are connected by a cingulum along their anterior margins; cusps are independent of the lophs, uniting when tooth is fully worn; H-pattern in the molars; m3 has a 2-cusped hypolophid. From Wood (1937).

Description— The p4 is smaller than m1, somewhat square in outline, and is quadrituberculate with two main cusps in each of the anterior and posterior lophs. Despite wear to the specimen, there is also a small but distinct accessory lophulid apparent between the protoconid and metaconid that is more closely appressed to the metaconid, and separated from the protoconid by a narrow gap. The origin of the lophulid is unclear due to the wear of the tooth, but it does appear to join with the protoconid at the anterolingual margin of the latter. A distinct, low anterior cingulum is present that begins anterior to the metaconid and terminates anterior to, and below, the lophulid-protoconid union. The metalophid is separated from the hypolophid by a straight, uninterrupted transverse valley. The hypolophid bears two cuspids, and there is a well-developed posterior cingulum across the width of the posterior margin of the tooth.

The m1 specimens vary in states of wear, allowing the progression of wear to be understood. In the least worn specimen, the metalophid bears a high, pointed metaconid, distinctly separated from a slightly lower protoconid of about equal size. An anterior cingulum borders the entire width of the metaconid. The anterior cingulum is then interrupted by an accessory crest that extends anterad from the protoconid, bending slightly linguad then recurving buccad, forming a "hairpin turn", and extending around the buccal edge. The anterior cingulum then terminates at a well-developed protostylid that partially interrupts the buccal end of the transverse valley. With wear, the protoconid expands anteriorly to join with the anterior cingulum, so that by the late stage of wear the "hairpin turn" is only visible with very close inspection. As wear increases, the cuspids of the metalophid become joined until they eventually form a single lophid that also incorporates the protostylid. On the hypolophid, the hypoconid and entoconid are of equal size and height to the protostylid, and are joined anteriorly by a low ridge. Unlike the holotype, a prominent posterior cingulum extends from the posterior of the entoconid across the posterior width of even the most worn hypolophid. This posterior cingulum then joins buccally to a low hypostylid that may be round or ovate in shape, and is recessed posteriorly to the rest of the hypolophid. The hypostylid is separated from the hypoconid by a narrow valley. With increased wear, the hypoconid and entoconid appear to join in a line that is parallel to the buccolingual axis of the tooth. With more advanced wear, the hypostylid is subsumed within the hypolophid. Eventually these cusps join the posterior cingulum and form a single lophid with no apparent valleys or cusps, as in the holotype. In even later wear, the protostylid and hypostylid almost appear to join, giving the occlusal surface of the m1 an almost U-shape.

Most of the m2 specimens are relatively worn, so that the original heights of all the cuspids are indeterminable, but the orientations of the individual cuspids and stylids are readily apparent. The m2 is differentiated from the m1 by a more transversely elongate appearance than in the m1, which is squarer in occlusal outline. The metalophid is similar to that of the m1, with clearly divided ovate protoconid and metaconid, joined anteriorly by a low ridge. No anterior cingulum is apparent on the anterolingual margin, but there is a hairpin turn-type cingulum extending from the

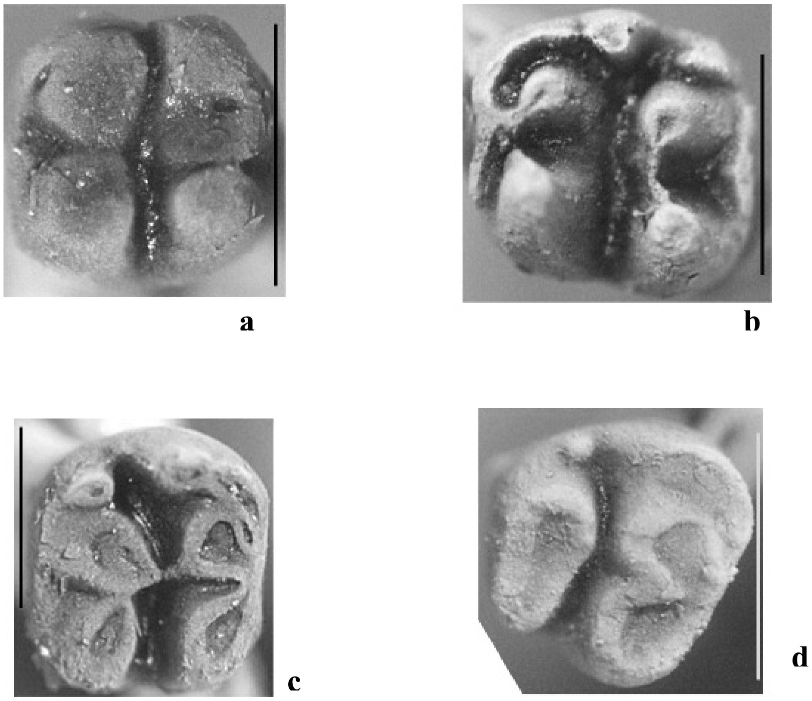


Figure 8.8 *Proheteromys nebraskensis*: a. SMNH P2521.210 Lp4; b. SMNH P2521.275 Rm1; c. SMNH P2521.081 Lm2; d. SMNH P2521.306 Lm3. Scale = 1mm, buccal to top of page.

protoconid that joins to the protostylid. On the hypolophid, the hypoconid and entoconid are joined anteriorly by a low ridge, and the hypoconid expands anterad into the transverse basin; with increased wear the hypoconid begins to connect to the posterior margin of the protoconid until eventually it creates the H-pattern on the occlusal surface, as described by Wood (1937) in the holotype. The weak posterior cingulum extends from the posterobuccal corner of the entoconid, eventually curving around the posterobuccal corner of the tooth to join with the round hypostyle.

The metalophid of the m3 is narrower than that of the m2 or m1, but is similar in morphology. The metaconid and protoconid are relatively high on unworn specimens, with little space between them. An anterior cingulum extends along the width of the metalophid and curves around the anterobuccal corner, terminating at the posterior margin of the metalophid where no protostylid is visible. The lingual-most portion of the anterior cingulum fades quickly with wear, leaving only a narrow ridge situated anteriorly to the protoconid that wraps around the anterobuccal corner. As wear progresses, the metaconid and protoconid become increasingly joined until they form a single, low metalophid. The metalophid is separated from the hypolophid by a transverse valley that does not appear to be interrupted at any point in wear. The

Table 8.6 Dental measurements of *Proheteromys nebraskensis*.

Tooth position	Dimension	N	Mean	OR	SD	CV
p4	AP	1	0.98			
	TRA	1	0.98			
	TRP	1	0.98			
m1	AP	9	1.19	1.10-1.28	0.07	5.96
	TRA	8	1.23	0.75-1.43	0.20	16.59
	TRP	7	1.20	0.88-1.43	0.16	12.95
m2	AP	3	1.23	1.15-1.28		
	TRA	3	1.38	1.30-1.48		
	TRP	2	1.30	1.25-1.35		
m3	AP	5	0.93	0.80-1.00	0.08	8.15
	TRA	5	1.00	0.88-1.00	0.08	8.32
	TRP	5	0.87	0.68-1.05	0.14	15.49

hypolophid is compressed transversely, extending from the lingual margin buccally to about halfway across the protoconid. The hypoconid dominates the posterior margin of the m3, with a smaller entoconid lingually and a very small hypostylid present buccally. As wear progresses, the entoconid and hypoconid join to form a single lophid that remains higher than, and separate from, the hypostylid, which is completely removed with sufficient wear. No posterior cingulum is clearly visible.

Discussion—The majority of undamaged specimens are within 10% of the described average sizes of *Proheteromys nebraskensis*, with some larger and some smaller. The only specimens that differ by greater than 10% are the m3 specimens, which are larger by about 14% anteroposteriorly and/or 13% transversely. This difference is considered minor, as a lower tooth row, SDSM 10001, figured by Green and Björk (1980) shows an m3 that appears smaller relative to the m2 than that of the holotype. As such, this tooth can probably be considered more variable in size than the other lower molars.

Although no uppers from the Rodent Hill Locality are referred to *P. nebraskensis*, Green and Björk (1980) figured an upper tooth row that was referred to this species. Korth (1989c) remarked that the upper dentition figured by Green and Björk (1980) was very similar to the holotype material of *Kirkomys milleri*, but no work has been published on the synonymy of these taxa. Comparison of the figure of SDSM 10001 in Green and Björk (1980) with photographs of F:AM 105537, the holotype of *K. milleri,* shows that these specimens are very similar; the M3 was the most disparate tooth in the tooth row but this alone may not indicate taxonomic separation because the dentition of *K. milleri* could be relatively variable. If they are synonymous, *P. nebraskensis* would be considered a florentiamyid based on the laterally compressed entostyle blocking the transverse valley of M1 on SDSM 10001 (Green and Björk, 1980), as this is considered a florentiamyid characteristic (Wahlert, 1983; 1984). A further line of evidence may be that twelve *Kirkomys milleri* uppers and eighteen *Proheteromys nebraskensis* lowers have been recovered together within the Rodent Hill fauna, which increases the likelihood that these belong to the same species. Most likely these species are synonymous, but the South Dakota material was not available for direct comparison, and no taxonomic revisions should be made until the specimens are compared directly.

9. FAMILY ZAPODIDAE

The family Zapodidae contains the modern jumping mice and birch mice, which are found in North America and Eurasia (Korth, 1994a). The family originated in the Bridgerian of North America (Emry and Korth, 1989), likely from a sciuravid ancestor (Korth, 1994a). The next record is from the Duchesnean (Kelly, 1992), and zapodids next appear in the Arikareean (Korth, 1994a). The greatest number of zapodid species appears in the Bridgerian (Korth, 1994a). Zapodids appeared later in Asia, in the late Eocene, and Europe, in the Oligocene (Korth, 1994a).

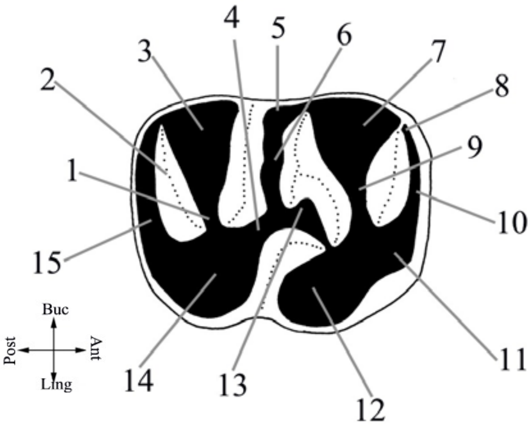


Figure 9.1 Generalized zapodid upper cheek tooth morphology, based on SMNH P2521.063 LM2? with major features identified. 1–metaloph 2—posterior fossette 3—metacone 4—endoloph 5—mesocone 6—mesoloph 7—paracone 8—accessory cusp 9—protoloph 10—anteroloph 11—anterocone 12—protocone 13—mesostyle 14—hypocone 15—posterior cingulum.

Drawn by Taran Meyer, modified by the author. Terminology from Wood and Wilson (1936) and Green (1977).

Modern zapodid skulls (no fossil skulls are known) are hystricomorphous, and the jaw is sciurognathous (Korth, 1994a).

The dental formula of zapodids is 1013/1003, and the P4 is lost in the living *Neozapus* (Korth, 1994a). The teeth of zapodids are brachydont to mesodont, and earlier species have well-defined cusps on the lophs of the teeth; the cusps of later zapodids are subsumed within the lophs (Korth, 1994a). The upper molars of zapodids (**Figure 9.1**) consist of five transverse lophs joining the cusps on either side of the tooth. There is usually a distinct mesocone, and an endoloph joins the lingual cusps (Korth, 1994a).

9.1 SYSTEMATIC PALEONTOLOGY

ZAPODIDAE Hemprich, 1820

SICISTINAE Allen, 1901

PLESIOSMINTHUS Viret, 1926

Type species—*Plesiosminthus schaubi* Viret, 1926

Referred species—*P. promyarion* Schaub, 1930; *P. myarion* Schaub, 1930; *P. clivosus* Galbreath, 1953; *P. quartus* Shevyreva, 1970; *P. huanguiensis* Li and Qiu, 1980; *P. lajeensis* Li and Qiu, 1980; *P. xiningensis*, Li and Qui, 1980; *P. winistoerferi* Engesser, 1987; *P. conjunctus* Ziegler, 1993; *P. moralesi* Sierra-Alvarez, Daams and Lacomba-Andueza, 1996; *P. tereskentensis* Lopation, 1999; *P. admyarion* Comte, 2000

Age and distribution—Middle to Late Oligocene and Miocene of Europe and Asia, Whitneyan to Hemingfordian of Great Plains of North America.

Diagnosis—Ectolophid of m1 joins protoconid obliquely (as opposed to joining the metalophid or protoconid via an anteroposterior lophid in *Schaubeumys*); weak mesoconid on m1 (strong in *Schaubeumys*); anteroconid smaller, less distinct in *Plesiosminthus*; protoloph on M1 (protolophule of Green, 1977) connects to the endoloph nearer the protocone in *Plesiosminthus* (joins nearer the mesoloph in *Schaubeumys*); metacone of M1 anteroposteriorly compressed with a straight metaloph in *Plesiosminthus* (rounded with curved metaloph in *Schaubeumys*). From Korth (1980) which contained a summary of diagnostic characteristics of the genus given by other authors that separate *Plesiosminthus* from *Schaubeumys* Wood, 1935b.

Korth (1980) also suggested that protocone and hypocone of M1 in *Plesiosminthus* were transversely compressed (as opposed to anteroposteriorly compressed in *Schaubeumys*) but this was disputed based on material described by Green (1992).

Discussion— In discussing the original material of North American *Plesiosminthus clivosus*, Galbreath (1953) remarked on the similarity of that species to the otherwise Old World genus. Several diagnoses of the genus *Plesiosminthus* have been produced, particularly to synonymize it with, or distinguish it from, *Schaubeumys* Wood, 1935b (Wilson, 1960; Martin, 1974; Engesser, 1979; Korth, 1980; Green, 1992; Korth, 1994a). The most recent treatment of these genera (Korth, 1994a) retains *Plesiosminthus clivosus* as the sole American species of the genus, while all other American species previously placed in *Plesiosminthus* are referred to the genus *Schaubeumys*.

Storer (2002) recorded the genus *Plesiosminthus* from the early Arikareean-age Kealey Springs Local Fauna in the Cypress Hills. Skwara (1988) described the species *P. clivosus* from the Hemingfordian-age Topham Local Fauna of the Cypress Hills as *Schaubeumys clivosus*.

PLESIOSMINTHUS SP.

Table 9.1, Figure 9.2

Referred specimen from Rodent Hill —SMNH P2521.063 (LM2)

Horizon at Rodent Hill—Collected in stratigraphically uncontrolled sampling.

Description—Dental terminology follows that from Green (1977), with these exceptions: the protolophule I and protolophule II of Green will be referred to here as the protoloph; and the metalophule I and metalophule II of Green will be referred to here as the metaloph. The tooth is longer than it is wide, a feature that is exacerbated by the sheared off buccal margin. The tooth is still recognizable despite this, with all lophs and cusps still plainly visible. Some features have a greatly widened appearance due to a high degree of occlusal wear. The anterior cingulum is low, slightly raised above the anterior transverse valley. A raised, slightly expanded accessory cusp is present on the

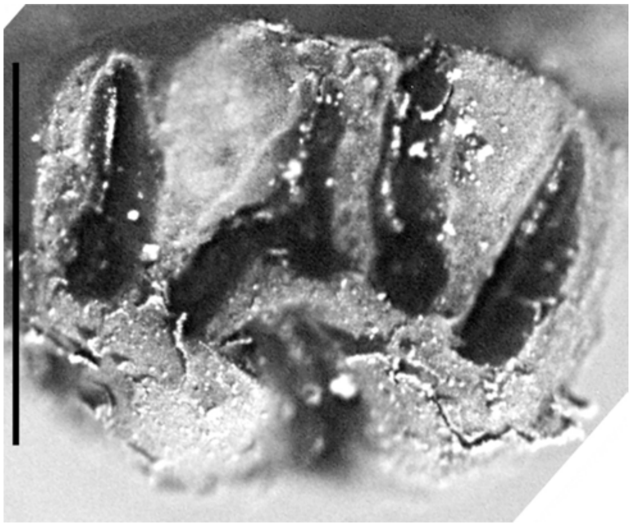


Figure 9.2 Plesiosminthus sp.: P2521.063 LM2?. Scale = 1mm, buccal to top of page.

buccal end of the anterior cingulum. On the lingual side, the anterior cingulum bends sharply, almost at 90°, and then terminates in a small, round anterocone. The protoloph extends buccally from the anterocone and expands into a large, anteroposteriorly compressed paracone. Further posterolingually from the anterocone is a slightly larger protocone. The endoloph extends from the anterobuccal side of the protocone to continue in a lingually concave curve that terminates at the hypocone. About midway along the endoloph, past the apex of the curve, a small mesocone is present as a tiny circular feature. The low mesoloph extends buccally from the mesocone and terminates in another very tiny widening representing the mesostyle. The mesostyle is nearly joined anteriorly with the much larger paracone; posteriorly the mesostyle is only slightly further away from the large metacone. Posteriorly along the endoloph from the mesocone, the metaloph extends buccally across the tooth, and then terminates in an anteroposteriorly-compressed metacone that is almost as large as the paracone, except lower and more compressed. Both the paracone and metacone are expanded at the buccal margin, giving both cusps a somewhat triangular outline. The endoloph terminates at the small, somewhat triangular hypocone posteriorly from the origin of the metaloph. Buccally from the hypocone, the posterior cingulum extends along the posterior margin, curving at the buccal end to join with the posterior margin of the metaloph. This union gives the posterior half of the tooth an enclosed posterior fossette that is transversely expanded, and crescentic in shape.

Table 9.1 Dental measurements of *Plesiosminthus* sp.

Tooth position	Dimension	N	Mean
M2	AP	1	1.55
	TRA	1	1.15
	TRP	1	1.13

Discussion—The tooth here described is identified as an M2 based on the position of the origin of the protoloph, and the enclosed posterior fossette (based on Text-Figure 1 in Green, 1972 pp. 97), and is referred to *Plesiosminthus* due to the compressed metacone, as opposed to an expected round metacone in *Schaubeumys* (see Genus Diagnosis). This feature is considered diagnostic for M1, but appears to be similar for M2 as well. More material, particularly a more diagnostic M1 or m1 from the same site, may aid in the clarification of this specimen. At that time, identification to the species level may also be feasible. It is notable that this specimen is larger than the Arikareean species *Plesiosminthus clivosus* by quite a wide margin. Based on dimensions for the lowers given by Galbreath (1953), the tooth is almost 50% longer and 30% wider. This would indicate that the Rodent Hill *Plesiosminthus* likely refers to a new species, but again more material is necessary.

10. STRATIGRAPHIC ASSESSMENT OF THE TAXA AND THE AGE OF THE RODENT HILL LOCALITY

10.1 AGE ASSESSMENT OF THE RODENT HILL LOCALITY

The Rodent Hill Locality had been assigned a preliminary Whitneyan age based on the leporids *Paleolagus* cf. *P. burkei* and *Megalagus primitivus*, the equid *Miohippus* near *M. equiceps* and the cricetid rodent *Eumys brachyodus* by Storer (1996) and Storer and Bryant (1997). The findings of Rothecker (2003) supported this assignment due to the occurrence of *Eumys brachyodus* in the same site as Orellan and Arikareean taxa.

Korth (1994a) and Rothecker (2003) have mentioned the relative lack of known Whitneyan rodents. This is more likely due to the relatively few known sites of this age compared to, for example, the Orellan or Arikareean (Emry *et al.*, 1987) than to an actual lack of diversity of rodent species during this particular NALMA. The following species from the families in this study have been identified in Whitneyan age faunas from sites other than Rodent Hill (referenced from Korth, 1994a, unless otherwise stated in brackets):

APLODONTIDAE

Prosciurus magnus

Campestrallomys siouxensis

Oropyctis pediasus

Haplomys liolophus

Sespemys thurstoni

Dakotallomys pelycomyoides (Tedrow and Korth, 1997)

Allomys storeri (Tedrow and Korth, 1997)

Leptoromys wilsoni (Tedrow and Korth, 1997)

SCIURIDAE

Cedromus sp.

? *Cedromus wilsoni* (Korth and Emry, 1991)

HELISCOMYIDAE

Heliscomys sp. (Tabrum *et al.*, 2001)

FLORENTIAMYIDAE

Kirkomys milleri

HETEROMYIDAE

Proheteromys nebraskensis

CASTORIDAE

Agnotocastor praetereadens

? *Palaeocastor nebrascensis*

Palaeocastor wahlerti (Korth, 2001a)

Oligotheriomys (Tabrum *et al.*, 2001)

ZAPODIDAE

NONE

As the above list indicates, some families are better understood from the Whitneyan than others. The Aplodontidae includes several Whitneyan species, while the Heliscomyidae has one tentatively referred taxon, and the Zapodidae have no previously described Whitneyan species. This low number of comparative species meant that several of the rodents identified at Rodent Hill might be new to Whitneyan faunas, and many were comparable with either an Orellan or Arikareean taxon (or sometimes both), indicating a transitional fauna between those two NALMA.

Table 10.1. Published temporal and geographic distribution of rodent taxa described from the Rodent Hill Locality. In the case of new species, or identification only to the genus, the distribution is given for the entire genus. (Continued on next page)

Taxon	Age	Geographic distribution
APLODONTIDAE		
Prosciurus parvus	Orellan	Nebraska Saskatchewan
Campestrallomys	Orellan-Arikareean	Nebraska Saskatchewan South Dakota
Haplomys liolophus	?Orellan-Whitneyan	? Saskatchewan Oregon
Dakotallomys pelycomyoides	Whitneyan	South Dakota
Pseudallomys	Orellan	Montana Saskatchewan
Parallomys	Arikareean	Nebraska Saskatchewan
SCIURIDAE		
Sciurion	Orellan-Arikareean Hemingfordian-Clarendonian	Saskatchewan Nebraska
Cedromus wilsoni	Orellan-Whitneyan	Wyoming
Nototamias	Arikareean-Hemingfordian	Nebraska South Dakota Saskatchewan Florida
Protospermophilus	Arikareean-Barstovian (Clarendonian?)	"western North America"

Table 10.1 lists the geographic and temporal distributions of the taxa described in this study from Rodent Hill. The Rodent Hill rodents have proven to be very diverse and indicate an assemblage unlike any described previously, so there is no one correlative site that shares all of the rodent genera recovered from the Rodent Hill Locality. Rothecker (2003) noted a number of similarities between the Rodent Hill Locality and the late Orellan Cedar Ridge Local Fauna described by Setoguchi (1978) based on the eomyids and cricetids. The rodents described in the present study do not support this; the only species identified from both localities are *Heliscomys vetus* and *Proheteromys* cf. *P. nebraskensis*. In fact, many of the families identified at Rodent Hill

are not described at all from Cedar Ridge, including the Florentiamyidae, Castoridae, Sciuridae and Zapodidae. Perhaps most significantly, Setoguchi (1978) described only two aplodontid species and neither species has been found at Rodent Hill. In general, many of the taxa at Rodent Hill are comparable to rodents from Nebraska and South Dakota, but there is no one site that best compares with the Rodent Hill Locality. It is possible that the faunas from these states are more similar to the Rodent Hill Locality

Table 10.1 (continued from previous page). Published temporal and geographic distribution of rodent taxa described from the Rodent Hill Locality. In the case of new species, or identification only to the genus, the distribution is given for the entire genus.

Taxon	Age	Geographic distribution
CASTORIDAE		
Agnotocastor praetereadens	Whitneyan	South Dakota
Oligotheriomys	Orellan, ?Whitneyan, ?Hemingfordian	North Dakota Montana Wyoming
Palaeocastorinae (*Palaeocastor)*	Whitneyan-earliest Arikareean	South Dakota North Dakota Oregon Saskatchewan
HELISCOMYIDAE		
Heliscomys vetus	Orellan	“Great Plains”
Heliscomys hatcheri	Orellan	“Great Plains”
Heliscomys	Duchesnean-Barstovian	Saskatchewan Wyoming Nebraska Montana South Dakota California
FLORENTIAMYIDAE		
Kirkomys milleri	Whitneyan	South Dakota
Ecclesimus	Orellan	Colorado Nebraska
HETEROMYIDAE		
Proheteromys nebraskensis	Orellan?-Whitneyan	?Wyoming Nebraska South Dakota
ZAPODIDAE		
Plesiosminthus	Arikareean-Hemingfordian	“Great Plains”

than are faunas from other areas in the Great Plains, but it is just as likely that this phenomenon is really due to the lower number of studied Whitneyan sites from other states (Emry *et al*., 1987). The White Hills Local Fauna of Montana may prove to be comparable as there are some taxa, such as *Oligotheriomys* and *Heliscomys*, which have also been identified from the Rodent Hill Locality, but the rodents of Montana have not yet been formally described. Rothecker (2003) also remarked on the similarities between the cricetids and eomyids of Rodent Hill and the White Hills Local Fauna.

Kirkomys milleri, *Proheteromys nebraskensis*, *Haplomys* cf. *H. liolophus*, *Dakotallomys* cf. *D. pelycomyoides*, and *Agnotocastor* cf. *A. praetereadens* are taxa that support a Whitneyan age (Rensberger, 1975; Wood, 1980; Wahlert, 1984; Korth, 1994a; Tedrow and Korth, 1997; Tedrow, 1999). The aplodontid *Campestrallomys*, the castorid subfamily Palaeocastorinae (likely *Palaeocastor*) and the sciurid *Cedromus* cf. *C. wilsoni* might also offer support of the Whitneyan age (Korth, 1989; Korth and Emry, 1991; Xu, 1996; Korth, 2001a), but the condition of the material makes definite identification uncertain. As is clear in **Table 10.1**, most of the species that would be indicative of a Whitneyan site have been described from South Dakota and/or Nebraska (Wahlert, 1984; Stirton, 1935; Wood, 1937; Korth, 1989a, 2001a; Tedrow and Korth, 1997), except for *Haplomys liolophus* from the John Day Formation of Oregon (Rensberger, 1975) and *Cedromus wilsoni* from the White River of Wyoming (Korth and Emry, 1991). *Prosciurus magnus* is an Orellan-Whitneyan species (Korth, 1989a) that was not recovered from Rodent Hill.

Several taxa were described that are better known from Orellan-age sites. One of these is the aplodontid *Prosciurus* cf. *P. parvus* from the Brule Formation of Nebraska (Korth, 1989a) and the Fossil Bush Locality of Saskatchewan (Meyer, 2003). Another aplodontid, the genus *Pseudallomys*, is previously described from the Fossil Bush Locality (Meyer, 2003) and the Dunbar Creek Formation in Montana (Korth, 1992), but those occurrences represent different species than at Rodent Hill. *Heliscomys vetus* and *Heliscomys hatcheri* are Rodent Hill heliscomyids that are normally associated with Orellan deposits (Wood, 1980). There are five Orellan species of *Heliscomys* (Korth, 1989c, 1994a), and one Arikareean species, *Heliscomys woodi* McGrew 1941. Setoguchi (1978) assigned a Whitneyan age to the Cedar Ridge Local Fauna of Colorado where *Heliscomys* cf. *H. vetus* was identified; however, Korth (1989b) reassigned that site to the late Orellan, a designation that is followed here. As such, the only record of the Heliscomyidae from the Whitneyan is the listed occurrence of the genus in the White Hills Local Fauna of Montana (Tabrum *et al.*, 2001), but only the genus *Heliscomys* is mentioned. The florentiamyid *Ecclesimus* has only been described from the Orellan of Colorado and Nebraska (Galbreath, 1948; Korth 1989c). The castorid *Oligotheriomys* has been listed from the Whitneyan of Montana (Tabrum *et al.*, 2001), but this genus is best known from the Orellan of North Dakota (Korth, 1998).

There are also several rodents from the Rodent Hill Locality that are previously known only from sites that are younger than Whitneyan. Among these, the aplodontid *Parallomys* has only been described in North America from the Harrison Formation of Nebraska (Korth, 1992) and the Kealey Springs Local Fauna of Saskatchewan (Storer, 2002), both of which are Arikareean age sites. The sciurid genera *Nototamias* and *Protospermophilus* and the zapodid *Plesiosminthus* are also known from sites that are Arikareean or younger (Korth, 1994a). The sciurid *Sciurion* was originally only known from sites that are Hemingfordian or younger (Skwara, 1986, 1988; Korth, 1998). This latter genus has now been recognized in the Orellan Fossil Bush Locality (Meyer, 2003) and the Arikareean Kealey Springs Local Fauna (Bell, Meyers and Bryant, *in prep*).

Given that there is a unique association of rodents at Rodent Hill that includes a mix of taxa previously considered characteristic of Orellan, Whitneyan, or Arikareean and younger, it suggests that the rodent fauna is transitional in nature, with more primitive (Orellan) taxa co-occurring during the same time period with more advanced (Arikareean, etc.) taxa. In this case, the intermediate age of the Rodent Hill taxa would be Whitneyan, which therefore supports the assignment of Storer and Bryant (1997) and Rothecker (2003). In fact, the transitional occurrence of the eomyid and cricetid rodents was part of the reason that Rothecker (2003) came to the conclusion that the site is Whitneyan.

10.2 THE RODENT HILL FAUNA IN THE CONTEXT OF THE CYPRESS HILLS

Among other sites in the Cypress Hills Formation, the Rodent Hill rodent fauna shares six taxa with the Fossil Bush Locality and seven taxa with the Kealey Springs Local Fauna. This finding parallels a statement made by Rothecker in an unpublished thesis (2003) that these three faunas share a number of taxa in the rodent families Eomyidae and Cricetidae.

The Fossil Bush Locality is part of the "titanothere section", like the Rodent Hill Locality, but is stratigraphically lower. Fossil Bush was designated an Orellan aged site by Storer (1996), but no taxa of the rodent families in this study were listed, with the exception of the aplodontid *Prosciurus relictus*. The aplodontid and sciurid rodents described by Meyer (2003) were consistent with an Orellan-age site. None of the other rodent families from Fossil Bush have been described in detail, which reflects the small number of taxa from that site in **Table 10.2**.

The Kealey Springs Local Fauna is located about 11 km northwest of the Rodent Hill Locality. The small mammals have been described by Williams and Storer (1998) and Storer (2002) and indicate an early Arikareean age for the site. Storer (2002) found that the fauna from Kealey Springs correlated well with the Monroe Creek assemblage from Nebraska and South Dakota. In addition to the 37 small mammals described at the Kealey Springs site by Storer (2002), two sciurids of the genus *Sciurion* have also been identified in the fauna (Bell, Meyers and Bryant, *in prep*). Storer (2002) previously identified the specimens in question as specimens of *Protosciurus* or *Nototamias*.

The rodent taxa (excluding the Cricetidae and Eomyidae) from the Fossil Bush, Rodent Hill and Kealey Springs Local Faunas are listed in **Table 10.2**. Prosciurine and allomyine aplodontids are found in all three sites, although there is a distinct shift from more primitive species at Fossil Bush to more advanced taxa at Kealey Springs, and there is a drop in overall diversity. Fossil Bush and Rodent Hill share the prosciurine genera *Prosciurus* and *Haplomys*. *Prosciurus* is represented by several more species at Fossil Bush than at Rodent Hill, while the species *Haplomys galbreathi* found at Fossil Bush is a more primitive species than *H. liolophus* from Rodent Hill (and possibly from Fossil Bush). The Orellan genus *Pelycomys* is found only at Fossil Bush, while the

Table 10.2. Occurrence of taxa of rodent families Aplodontidae, Sciuridae, Heliscomyidae, Heteromyidae, Florentiamyidae, Castoridae and Eutypomyidae in the Fossil Bush, Rodent Hill and Kealey Springs Local Faunas. Fossil Bush taxa based on Storer (1996) and Meyer (2003); Kealey Springs taxa based on Storer (2002).

TAXON	FOSSIL BUSH LOCAL FAUNA	RODENT HILL LOCAL FAUNA	KEALEY SPRINGS LOCAL FAUNA
APLODONTIDAE			
Prosciurinae	X	X	X
Prosciurus relictus	X		
Prosciurus magnus	X		
Prosciurus parvus	X	X	
Haplomys galbreathi	X		
Haplomys liolophus	?	X	
Campestrallomys annectens	X		
Campestrallomys sp.		X	
Campestrallomys cf. *C. dawsonae*			X
Pelycomys	X		
Dakotallomys		X	
Pseudallomys	X	X	
Parallomys		X	X
Downsimus			X
Alwoodia			X
SCIURIDAE			
Sciurion xenokleitus	X	X	X
Sciurion oligocaenicus	X	X	X
Cedromus		X	
Nototamias		X	X
Protospermophilus		X	X
Protosciurus			X
HELISCOMYIDAE			
Heliscomys		X	
FLORENTIAMYIDAE			
Kirkomys		X	
Ecclesimus		X	
Hitonkala			**X**
Florentiamys			**X**
HETEROMYIDAE			
Proheteromys nebraskensis		**X**	
Proheteromys ironcloudi			**X**
Schizodontomys			**X**
ZAPODIDAE			
Plesiosminthus		X	X
CASTORIDAE			
castorid spp.		X	X
EUTYPOMYIDAE			
Eutypomys spp.	X		X

Whitneyan *Dakotallomys* occurs at Rodent Hill. The allomyine *Pseudallomys* is described from both sites as well. None of the above aplodontids are described from Kealey Springs. A genus that is shared by all three sites is *Campestrallomys*, although the Kealey Springs species is more advanced than the Fossil Bush species. The Rodent Hill *Campestrallomys* is an indeterminate species, but seems to have a mix of primitive traits such as a reduced ectoloph, and advanced traits such as the dominance of the buccal cusps. The more advanced allomyine genus *Parallomys* is shared only between Rodent Hill and Kealey Springs, although the species are not the same. Kealey Springs is the only site where the advanced taxa *Downsimus* (a prosciurine) and *Alwoodia* (an allomyine) are present.

The only other rodent taxa described from Fossil Bush are the sciurids *Sciurion xenokleitus* and *S. oligocaenicus*, and these two species are found in both the Rodent Hill Local Fauna and the Kealey Springs Local Fauna.

The Eutypomyidae has been described from Fossil Bush and Kealey Springs but not Rodent Hill. Although this family is known from other Whitneyan faunas (Korth, 1994a), no taxa of this family are described for Rodent Hill. It is possible that some of the tooth fragments assigned to the family Castoridae might actually be eutypomyids, but fragmentary remains are difficult to identify.

The other families of rodents have not been described in detail from Fossil Bush, making meaningful comparisons between that site and Rodent Hill and Kealey Springs impossible at this time.

Between Rodent Hill and Kealey Springs, there are some trends, such as the constant diversity, but not taxa, within the families Sciuridae, Florentiamyidae and Zapodidae. There is also the increase in heteromyid diversity from Rodent Hill to Kealey Springs, and the total lack of heliscomyids in the latter.

Table 10.3. Occurrence of Rodent Hill rodent taxa in each stratigraphic unit. N/A refers to species that were not recovered stratigraphically

Taxon	**Stratigraphic Unit**				
	Unit I	**Unit II**	**Unit VI**	**Unit VII**	**N/A**
Aplodontidae					
Prosciurus cf. *P. parvus*					**X**
Prosciurus sp. 1 & sp. 2					**X**
Campestrallomys sp.					**X**
Haplomys cf. *H. liolophus*			**X**		
Dakotallomys pelycomyoides	**X**				
Pseudallomys korthi	**X**	**X**			
Parallomys sp.					**X**
Sciuridae					
Sciurion oligocaenicus	**X**				
Sciurion xenokleitus	**X**	**X**	**X**		
Cedromus cf. *C. wilsoni*			**X**		
Nototamias sp.					**X**
Protospermophilus sp.					**X**
Castoridae					
Agnotocastor *cf.* A. praetereadens					**X**
? *Oligotheriomys*				**X**	
? Palaeocastorinae sp.					**X**
Castoridae indet.	**X**				
Heliscomyidae					
H. (Syphyriomys) hatcheri	**X**	**X**	**X**		
H. (Syphyriomys) sp.					**X**
Heliscomys (Heliscomys) vetus	**X**		**X**	**X**	
Florentiamyidae					
Kirkomys milleri	**X**				
Ecclesimus sp.	**X**		**X**	**X**	
Heteromyidae					
Proheteromys nebraskensis	**X**			**X**	
Zapodidae					
Plesiosminthus sp.					**X**

The stratigraphic position of the Rodent Hill Locality above the Orellan-aged Fossil Bush Locality, and the more advanced nature of the aplodontid taxa, suggest that

Rodent Hill is a younger site. The rodent taxa of Rodent Hill are generally less advanced than those of the early Arikareean aged Kealey Springs, and this implies that Rodent Hill is a relatively older site. This intermediate position of the Rodent Hill Locality is strong, if indirect, evidence that supports Whitneyan age designation of the fauna.

10.3 STRATIFICATION OF TAXA WITHIN THE RODENT HILL LOCALITY

Thirty-five fossil teeth, representing thirteen of the twenty-three taxa identified, were recovered from the designated stratigraphic units at the Rodent Hill site. These teeth were used to determine any differences between the rodent taxa at the bottom of the site and those at the top (**Table 10.3**). The results are inconclusive.

The presence of taxa such as *Kirkomys milleri* and *Proheteromys nebrascensis* in Unit I is good evidence that the bottom of the site represents a Whitneyan fauna; since *P. nebrascensis* is also found in Unit VII, the top unit should also be considered Whitneyan.

The differences between the upper and lower stratigraphic units are not conducive to interpreting evolutionary changes in the Rodent Hill fauna at this time. Future tests of stratification at Rodent Hill should involve collection of even larger amounts of matrix for processing, and groups other than rodents should also be studied to look for patterns in the taxa present in the units. At the minimum, enough fossil material should be recovered *in situ* to represent all of the known rodent taxa, as some appear to be relatively rare. Once these rare taxa are recovered *in situ*, it could be assumed that a more accurate representation of the rodent fauna from the Rodent Hill site has been obtained. In turn, any stratification of taxa within the Rodent Hill site might then be considered to give a more accurate picture of evolutionary changes in the fauna in the time represented at Rodent Hill.

10.4 THE RODENTS OF THE WHITNEYAN NALMA

Presuming that the Rodent Hill Locality is a Whitneyan site, the rodents described from the Rodent Hill Locality will affect the faunal characterization of the

Hemingfordian, Arikareean, Whitneyan and Orellan land mammal ages. Previous last and first appearances are taken from Korth (1994a) except where noted.

Last appearance in the Orellan is no longer valid for the following taxa: *Pseudallomys, Ecclesimus, Heliscomys vetus, H. hatcheri* and possibly *Prosciurus parvus*. All of these taxa have now been identified in a Whitneyan-age site, and they should now be considered to have a Whitneyan last appearance. The genus *Cedromus* has only been tentatively assigned to a Whitneyan site (Korth and Emry, 1991), and the recovery of this genus from Rodent Hill provides further support that the last appearance of this genus is also in the Whitneyan.

The first appearance in the Arikareean is no longer valid for the following taxa: *Nototamias, Protospermophilus, Plesiosminthus* and *Parallomys*. These genera all occur in the Rodent Hill Locality, and so their first appearance should be considered Whitneyan.

The genus *Sciurion* no longer has a first appearance in the Hemingfordian. This genus has now been recovered in Orellan, Whitneyan and Arikareean sites in the Cypress Hills, and so the first appearance of the genus should be Orellan.

Proheteromys nebraskensis, Kirkomys milleri, Dakotallomys pelycomyoides, Haplomys liolophus and *Agnotocastor praetereadens* remain useful as characteristic species for the Whitneyan. The first appearance of the Palaeocastorinae may still be in the Whitneyan.

10.5 SUMMARY

A Whitneyan North American Land Mammal Age is supported for the Rodent Hill Locality based on comparisons with taxa from other North American sites and with faunas from other sites in the Cypress Hills Formation.

Species that indicate that the Rodent Hill Local Fauna is advanced over Orellan age sites include *Proheteromys nebrascensis, Kirkomys milleri, Dakotallomys pelycomyoides, Haplomys liolophus* and *Agnotocastor praetereadens*, as well as several genera that were previously known only from Arikareean and younger sites. Similarly, the Rodent Hill Local Fauna is older than Arikareean sites based on the presence of Orellan taxa including *Heliscomys hatcheri* and *H. vetus*, *Prosciurus parvus, Ecclesimus* and *Pseudallomys*. The faunal composition of the Rodent Hill Locality is transitional between the Orellan-age Fossil Bush Locality and the early Arikareean-age Kealey Springs Local Fauna, indicating an intermediate age.

The stratigraphic position of the Rodent Hill Locality in the “titanothere section” also lends support to the Whitneyan age of the site. The Rodent Hill Locality is above the Orellan-age Fossil Bush Locality, and below an unnamed Hemingfordian-age site that caps the top of the section.

11. IMPLICATIONS OF STUDY

11.1 EVOLUTIONARY IMPLICATIONS: THE RODENTS OF THE RODENT HILL LOCALITY

11.1.1 Aplodontidae

Prosciurus cf. *P. parvus, Prosciurus* spp. indet.

The presence of *Prosciurus parvus* in the Rodent Hill Local Fauna is the youngest record of the species, which is previously described from the Orellan of Nebraska and Saskatchewan (Korth, 1989a, b; Meyer, 2003). The Rodent Hill species is very similar in overall appearance and size to the Orellan specimens except for the doubled metaconule on the P4. There are few specimens of this taxon at Rodent Hill, but this difference could indicate a variation within the species, or it may be an evolutionary change in the morphology of the Whitneyan specimens from the older Orellan material.

The two other *Prosciurus* specimens from Rodent Hill are single teeth that are difficult to assign. One specimen (P2521.212) is substantially smaller than any other *Prosciurus* taxon. The other specimen (P2521.399) is larger than the *Prosciurus* cf. *P. parvus* specimens from Rodent Hill, but the condition of the tooth makes specific identification impossible.

Campestrallomys sp. indet.

This genus has been described from the Orellan (Meyer, 2003) and early Arikareean (Storer, 2002) of the Cypress Hills. Only one specimen that is referable to this genus was found at Rodent Hill. The incomplete ectoloph is reminiscent of the Orellan species *C. annectens*; while the pronounced buccal cusps is more characteristic of the Whitneyan species *C. siouxensis*. More specimens will be necessary to identify the Rodent Hill species and assess the evolutionary implications of the apparently intermediate morphology observed.

Haplomys cf. *H. liolophus*

The species *Haplomys liolophus* was previously known only from the Whitneyan levels of the John Day Formation in Oregon (Rensberger, 1975) although the genus is present in the Orellan of South Dakota (Tedrow and Korth, 1997) and the middle Oligocene of Kazakhstan and Mongolia (Shevyreva, 1971). The Rodent Hill material does not appreciably differ from the John Day material and so there is no further information on the morphology of the species provided by the Rodent Hill specimens.

Dakotallomys cf. D. pelycomyoides

The recovery of a Dakotallomys pelycomyoides from the Cypress Hills is the northernmost presence of this species, as it has previously only been described from South Dakota (Tedrow and Korth, 1997). The identification of the species is due to the diagnostic buccal cingulum present on the m2 and the relatively large size. The lowers of this species from Rodent Hill do not differ significantly from the South Dakota material.

The first upper teeth for Dakotallomys have been described from Rodent Hill. The uppers are very similar to those of Pelycomys, except for the presence of a weak ectoloph that is lacking in Pelycomys. The large size of these upper molars represents the largest aplodontid at Rodent Hill, and is another reason these teeth are referred to Dakotallomys. Tedrow and Korth (1997) suggested that Pelycomys, Dakotallomys and another genus, the Uintan to Chadronian Spurimus, might share a close enough ancestry to be considered a separate clade within the prosciurines, but they wanted to wait for uppers of Dakotallomys to be recovered. Since only the P4 and M3 are known from Rodent Hill, the upper M1/M2 of Dakotallomys should be described before these genera are grouped supergenerically from the other prosciurines.

Pseudallomys korthi

Pseudallomys korthi is the youngest occurrence of the genus Pseudallomys, previously recorded only from the Orellan of Montana (Korth, 1992a) and Saskatchewan (Meyer, 2003). Pseudallomys nexodens was described based on a single lower tooth row, with no uppers (Korth, 1992a). Meyer (2003) described uppers for an unnamed species from the Fossil Bush Locality and upper teeth are also found at the Rodent Hill Locality.

The Rodent Hill species approximates the size of Fossil Bush Pseudallomys closely, but the occlusal pattern is more like Pseudallomys nexodens. This is especially true of the distinctive enamel crenulations found in the basins of the lower teeth of all members of the genus. In Fossil Bush Pseudallomys, the crenulations are thick and numerous; in P. nexodens and P. korthi, the crenulations appear to be fewer in number and thinner. The cusps of Fossil Bush Pseudallomys also appear to generally be more robust than in the other two species. More material of the genotypic species is necessary for proper comparisons, but it appears that the Rodent Hill species of Pseudallomys may actually be morphologically closer to the Montana species P. nexodens than to the Fossil Bush species. This could indicate that the Fossil Bush Pseudallomys was not the ancestor of the Rodent Hill species, but instead was out competed by a smaller descendent of the Montana species in the Cypress Hills during the Whitneyan. Alternatively, the Fossil Bush Pseudallomys may have evolved a morphology that was similar to that of P. nexodens during the Whitneyan. Fossil material of these species from other areas may help to resolve this question.

Parallomys

Only one tooth of this genus was recovered from the Rodent Hill Locality. This is the first time the genus has been described from a Whitneyan site. Parallomys has previously been described from the Arikareean of Nebraska (Korth, 1992b) and Saskatchewan (Storer, 2002) as well as the Late Oligocene of Europe (Rensberger, 1983). The Rodent Hill specimen is smaller than other Parallomys specimens, but is otherwise very similar in morphology.

11.1.2 Sciuridae

Sciurion xenokleitus and *S. oligocaenicus*

These two species are the most common squirrels at the Rodent Hill Locality. They represent a genus that was previously known only from the Hemingfordian of Saskatchewan (Skwara, 1986; 1988) and the Clarendonian of Nebraska (Korth, 1998).

The Sciurion species found at Rodent Hill are also known from the Orellan Fossil Bush Locality (Meyer, 2003) and the early Arikareean Kealey Springs Local Fauna. The two species are very distinct from one another, but there are only minor intraspecific variations in the fossils from the oldest Orellan material to the youngest Arikareean specimens. It is remarkable that two related rodent species would persist for such a long period of time (~ 12 Ma) with little appreciable change. It is possible that, if skeletal material were available, differences between populations would be discernable. With the information currently available, it appears that a pair of long-lasting sciurid species was present in the Cypress Hills during the Oligocene. By the Hemingfordian, the larger species Sciurion xenokleitus is extinct with no descendants; the smaller S. oligocaenicus has been replaced by the species S. campestre that is markedly different in tooth proportions.

Skwara (1986) assigned the genus Sciurion to the flying squirrel subfamily Pteromyinae based on morphological similarity to the genus Blackia Mein, 1970. Although their affinities within the pteromyine squirrels are unknown, the relationship between Sciurion and Blackia is not in dispute. It is a relatively simple exercise to provide an ancestor-descendant path from Sciurion to Blackia. Sciurion first appears in the Orellan of North America (Meyer, 2003); Blackia is a later species, first appearing in the late Oligocene of Europe (Mein, 1970; de Bruin, 1999) and the Hemingfordian of North America (Hutchison and Lindsay, 1974). The two genera differ in the presence of an anteroconid and more distinct stylid cusps in Sciurion that are reduced in Blackia (Skwara, 1986; Mein, 1970).

Additional fossil remains, particularly skeletal elements, would be useful for determining how, if at all, these two genera relate to other flying squirrels, or if their similar dental morphology, particularly the crenulated enamel of the tooth basins, indicates convergence.

Cedromus cf. *C. wilsoni*

The presence of this taxon at Rodent Hill gives support that this species, or one very similar to it, was present in the Whitneyan. Korth and Emry (1991) described *Cedromus wilsoni* and tentatively assigned it to either Orellan or Whitneyan age. It is possible *Cedromus wilsoni* is found in both ages. Since only one worn specimen was found at Rodent Hill more material is necessary to draw conclusions.

The genus *Cedromus* appears for the first time in Saskatchewan, extending the geographic range of the subfamily Cedromurinae further north than the previous known range of Nebraska and Wyoming (Korth and Emry, 1991).

Nototamias

The presence of *Nototamias* at Rodent Hill is the earliest occurrence not only of the genus, but also of the tribe Tamiini. *Nototamias* has been described previously from the Arikareean of Saskatchewan (Storer, 2002).
The two teeth that represent this genus from Rodent Hill are very similar in size and morphology to later species of the genus, but the teeth were worn, making a specific identification difficult.

Protospermophilus

This genus is represented at the Rodent Hill Locality by only two teeth, but they are representative for the genus (see Discussion in Sciuridae chapter). The Rodent Hill material is smaller than any other *Protospermophilus* teeth. The presence of this genus in the Whitneyan is an earlier first appearance of the genus, and this also extends the first appearance of the tribe Marmotini into the Whitneyan. The genus has been recovered from Saskatchewan previously in the Arikareean (Storer, 2002) and the Hemingfordian (Skwara, 1988).

11.1.3 Castoridae

Agnotocastor cf. *A. praetereadens*

The presence of *Agnotocastor praetereadens* in Saskatchewan is the northernmost occurrence of the species. The fossil material from the Rodent Hill Locality is limited and does not generally enhance the understanding of the evolution of this species.

This species is considered indicative of Whitneyan faunas (Emry *et al*., 1987; Prothero and Whittlesey, 1998), so the presence of this species at Rodent Hill was an important age indicator for the site.

?*Oligotheriomys*

The identification of this genus from the Rodent Hill Locality is tentative because it is based on one tooth. The genus has been recorded from the Whitneyan of Montana (Tabrum *et al.*, 2001) but this is the first potential record of the genus from Saskatchewan. Little can be determined about morphological trends in this genus based on the Rodent Hill specimen, except that it is appreciably smaller than the Orellan species *Oligotheriomys primus*.

?Palaeocastorinae, gen. et sp. indet.

Storer (1996) referred castorid dentition to the Palaeocastorinae from the Kealey Springs Local fauna. Storer (2002) did not follow this designation and instead left the castorids from that site as indeterminate. Nonetheless, the presence of the subfamily at Rodent Hill is not the first record in Saskatchewan, although it is the earliest record.

The possible presence of this subfamily in a Whitneyan deposit does not contradict the age assignment of the site, as the species *Palaeocastor nebrascensis* is referred to as a late Whitneyan age species by Xu (1996), and the species *P. wahlerti* is a Whitneyan species described by Korth (2001a).

11.1.4 Heliscomyidae

Heliscomys (Heliscomys) vetus, H. (Syphyriomys) hatcheri, H. (Syphyriomys) sp.

The presence of three species of *Heliscomys* in a Whitneyan site is the second record of any species from this age. The only other record of *Heliscomys* in the Whitneyan is the listed presence of the genus in the White Hills Local Fauna of Montana (Tabrum *et al.*, 2001).

These species fill in a major gap in the record of the Heliscomyidae, which is known from 7 species in the Orellan (Korth, 1989c; 1994a) and one in the Arikareean. Korth (1994a) presumed that the family was present during this time, but had not been described. The three Rodent Hill species support the trend of the decline in diversity of the heliscomyids before their extinction during the Arikareean.

The specimens of *Heliscomys (H.) vetus* and *H. (S.) hatcheri* from Rodent Hill are morphologically very similar to their Orellan conspecifics. The only major difference is a small increase in size of both species from the Orellan to the Whitneyan Rodent Hill specimens. This small variation is interpreted as a minor change within the species over an appreciable span of time.

The third Rodent Hill *Heliscomys* is an indeterminate species differentiated by its larger size from most other heliscomyids. The interrupted lingual cingulum of the M1-2 indicates a placement within the *Heliscomys (Syphyriomys)* subgenus that also includes *H. (S.) hatcheri*.

11.1.5 Florentiamyidae

Kirkomys milleri

The Rodent Hill Locality specimens assigned to *Kirkomys milleri* do not differ appreciably from those described by Wahlert (1984) so they do not add any new information about the morphology of the species.

The presence of this species in Saskatchewan is the northernmost occurrence of the species, as it was previously recorded only from the Whitneyan of Nebraska (Wahlert, 1984).

Ecclesimus

The occurrence of *Ecclesimus* at Rodent Hill is the first Whitneyan record of this genus. The only known species, *E. tenuiceps* has been found in Orellan sites (Korth, 1989c). This is also the first time the genus has been recorded in Saskatchewan. There is the possibility that the Rodent Hill *Ecclesimus* is a distinct species from *E. tenuiceps*, but geomyoid rodents are difficult to diagnose based on isolated teeth.

The first lowers for the genus are described from the Rodent Hill Locality. The assignment of these teeth to *Ecclesimus* is based primarily on their size since they are larger than any of the heliscomyid taxa described, but smaller than those assigned to *Proheteromys nebraskensis*.

Korth (1993) determined that *Ecclesimus* is a sister taxon to most of the later genera of florentiamyids—*Florentiamys, Sanctimus* and *Fanimus*. Previously, *Ecclesimus* was recorded only from the Orellan (Korth, 1989c), while the record of these later florentiamyids begins in the Arikareean, so the Rodent Hill *Ecclesimus* fills in a temporal gap in the record of this lineage. The relationships are based on skull characteristics and the morphology of the P4 compared to the M1. In *Florentiamys, Sanctimus* and *Fanimus* the P4 is molariform and larger than the M1 (Korth, 1993). Like *Ecclesimus tenuiceps*, the Rodent Hill *Ecclesimus* has a P4 that is not molariform, and is smaller than M1, so the Whitneyan species does not demonstrate the later dental advancement of the other florentiamyids.

11.1.6 Heteromyidae

Proheteromys nebraskensis

Morphologically, the teeth assigned to *P. nebraskensis* are very similar to those described previously (Wood, 1937; Green and Björk, 1980; Tedrow, 1999). This is the first time the species has been described from Saskatchewan.

11.1.7 Zapodidae

Plesiosminthus

This is the first identification of this genus in a pre-Arikareean site. Only one tooth has been recovered, so a confident specific identification cannot be made.

The specimen is interesting because it is appreciably larger than the Arikareean *Plesiosminthus clivosus*, based on dimensions from Galbreath (1953). The size of this tooth would suggest that the Rodent Hill specimen belongs to a different species, but one tooth is not a sufficient basis for a diagnosis. The large size of the Whitneyan zapodid is interesting, particularly considering that some of the other Rodent Hill taxa, including *Pseudallomys, Parallomys* and *Protospermophilus*, are smaller at this site than at any other time or place. The implications of these allometric differences are unknown.

11.2 RODENT DIVERSITY IN THE WHITNEYAN NALMA

The published record of most rodent families from the Whitneyan is limited (Korth, 1994a), especially when compared to the preceding Orellan age and the succeeding Arikareean age. Of the families present at that time, only the Aplodontidae have an extensive record, while the Sciuridae, Florentiamyidae, Heteromyidae, Heliscomyidae and Castoridae have few documented species, and the Zapodidae has no documented species (Korth, 1994a). Rothecker (2003) discussed the diversity of the Whitneyan eomyid and cricetid rodents.

Emry *et al.* (1987) noted the paucity of Whitneyan sites compared to the Orellan and Chadronian, and while additional sites have been identified since then (Storer, 1996; Tabrum *et al.*, 2001) the number of sites remains low. As noted by Rothecker (2003), the low rodent diversity apparent in the Whitneyan is not due to a decline in rodent species, but reflects this low number of Whitneyan microsites that have been described in detail.

As with the Eomyidae and Cricetidae (Rothecker, 2003) the diversity within the rodent families of this study are more diverse than previously recorded. This is due to the extension of the temporal range of several taxa including *Pseudallomys*, *Ecclesimus, Heliscomys hatcheri, H. vetus*, *Prosciurus parvus*, *Parallomys, Protospermophilus, Nototamias,* and *Plesiosminthus*.

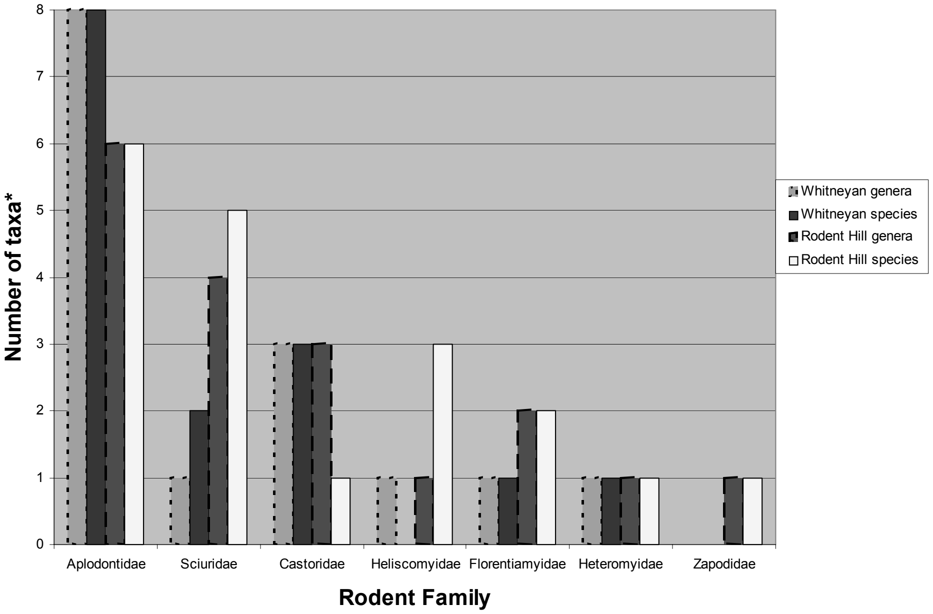
The most diverse rodent family (**Figure 11.1**) at Rodent Hill is the Aplodontidae with 6 genera representing at least 6 species. This number appears to be lower than the diversity known for the aplodontids from other sites, but three of the Rodent Hill taxa

(*Parallomys, Pseudallomys korthi, Prosciurus* cf. *P. parvus*) are described from the Whitneyan for the first time, and four previously described aplodontids (*Prosciurus magnus, Oropyctis pediasus, Allomys storeri, Leptoromys wilsoni*) were not identified at Rodent Hill. This means that the total number of Whitneyan aplodontid species is 11, a higher diversity than that of any other rodent family during this time (Korth, 1994a; Rothecker, 2003).

The peak of diversity of the Aplodontidae is in the Arikareean (Korth, 1994a) with at least 20 species; most represent the more advanced subfamilies Meniscomyinae and Allomyinae, but a few prosciurines are present. The Orellan has a similar number of aplodontid taxa to the Whitneyan (Korth, 1994a; Tedrow and Korth, 1997; Meyer, 2003) with 7 genera and 10 species, and all are prosciurines except possibly *Pseudallomys* (Meyer, 2003). The presence of this many taxa in the Orellan and Whitneyan may indicate a more gradual diversification of the aplodontids than previously realized.

Figure 11.1. Rodent diversity previously described from Whitneyan sites in North America and from the Rodent Hill Local Fauna.

*Numbers taken from Korth (1994a) for all families; also Tedrow and Korth (1997) for the aplodontids; Korth and Emry (1991) for the sciurids; Tabrum *et al.* (2001) for the heliscomyids and castorids; Korth (2001a) for the castorids.



More sciurid genera are recovered from the Rodent Hill Locality than previously recorded (**Figure 11.1**). The Sciuridae during the Whitneyan are almost equal in number of species to the sciurids of the Orellan and Arikareean (Korth, 1994a), which could indicate an evolutionary stasis before the family diversified greatly in the Hemingfordian and Barstovian (Korth, 1994a).

Among the geomyoids, the Heteromyidae are represented by the only previously recorded Whitneyan species, *Proheteromys nebraskensis*. The florentiamyids are represented by one more genus than previously known (**Figure 11.1**), which makes the family more diverse during the Whitneyan than during the Orellan (Korth, 1994a). This number of taxa is still very low compared to the diversity of the family in the Arikareean, where 5 genera and 10 species of florentiamyids have been identified (Korth, 1994a). The heliscomyids are represented in the Whitneyan at Rodent Hill by 3 distinct species. Although the genus *Heliscomys* has previously been listed from the Whitneyan (Tabrum *et al.*, 2001), these are the first heliscomyid species described from the age. The number of Rodent Hill species fits in well with a trend of declining diversity in the family seen from the Orellan, with 3 genera and 5 species, to the single genus and species found in the Arikareean and Barstovian (Korth, 1994a).

Three castorid genera (one indeterminate, but distinct from the others) have been found in the Whitneyan Rodent Hill Local Fauna (**Figure 11.1**). The two identifiable genera (*Agnotocastor, Oligotheriomys)* have been previously identified from the Whitneyan (Korth, 1994a; Xu, 1996; Tabrum *et al.*, 2001) including the species *Agnotocastor* cf. *A. praetereadens*. The third Rodent Hill castorid, a palaeocastorine of indeterminate genus, is in keeping with previous assignments of palaeocastorines from the Whitneyan (Xu, 1996; Korth, 2001a). The Whitneyan record of castorids is less diverse than that of the Orellan, which has 2 genera but at least 3 species (Korth, 1994a; 1998, 2001a), and there are substantially fewer Whitneyan taxa compared to the castorid maximum diversity in North America of 7 genera and 14 species seen in the Arikareean (Korth, 1994a; Korth and Rybczynski, 2003).

The Zapodidae has not been described from any Orellan or Whitneyan locality before (Korth, 1994a) although there are tentative North American records of the family as far back in time as the Bridgerian (Emry and Korth, 1989). The family increases in diversity from the one taxon in the Whitneyan to a maximum of 4 genera and 6 species in the Barstovian (Korth, 1994a).

Korth (1994a) mentioned that only 14 species of rodents were known from the Whitneyan; recent studies (Tedrow and Korth, 1997; Tabrum *et al.*, 2001; Rothecker, 2003) have supported the notion that the diversity of Whitneyan rodents was higher. Including those other studies and this one, the current number of Whitneyan rodents is about 35 species. This number is still low compared to the Orellan with at least 48 species and the Arikareean with over 100 species (Korth, 1994a) but the representation of the rodent families in North America during the Whitneyan is improving, so that most families that are known from the Orellan and Arikareean have now been described from the Whitneyan as well.

11.3 PALEOENVIRONMENTAL IMPLICATIONS: THE RODENTS AND SEDIMENTOLOGY OF THE RODENT HILL LOCALITY

There is little direct evidence at the Rodent Hill Locality for the climate during the Whitneyan. There is no phytolith, palynomorph or coal data present, and there is no fossil plant material available to give clues to the local flora. As well, the record of paleobotanical data from Whitneyan sites is generally poor, with only one site listed by Wing (1998) from the Upper Ruby River of Montana (Becker, 1961). The apparent similarities between Rodent Hill and the White Hills Local Fauna of Montana may allow the assumption that the local paleoecology was similar. For the most part, the area may have been somewhat cooler and drier than the Orellan (Wing, 1998) with wooded areas consisting of conifers and broadleaf deciduous trees (Becker, 1961).

The teeth of the rodents at Rodent Hill are good indicators that grasses were probably not yet prevalent. Where grass is prominent, the teeth of grazing mammals have to deal with excessive wear caused by the silca in grasses which often results in more hypsodont teeth (Romer, 1962, p. 315). The teeth of most of the rodent families at

Rodent Hill are rooted and brachydont, and even the higher-crowned castorids are low-crowned compared to later forms (Korth, 1994a) indicating diets of softer plant matter that do not contain phytoliths.

The sediment in the area may also indicate a climate that was variably dry at times. As mentioned in **Chapter 2**, the stratigraphic sequence of Rodent Hill indicates an alternation of wetter periods of sediment deposition with comparatively drier periods of nodule accretion. The wet events are indicated by the sand bar units that were deposited by fluvial activity. Although there is no direct evidence at the site, it is reasonable to assume that the presence of a stream in the area would encourage a greater amount of plant life (and by extension, animal life).

The nodular units indicate drier periods when moisture was low (but probably not absent). During these periods of time the plant life may have been under greater stress, resulting in fewer, more resilient plants.

Although the evidence is tenuous due to small sample numbers, the fossils recovered from the stratigraphic units follow a distinct pattern that is related to the alternation of sediments seen in the sedimentology (**Table 11.1**). More fossils were recovered in each of the sandier units than in the nodular layers closest to them. It is possible that the higher moisture levels indicated in the fluvial units may have supported a higher number of species and individuals, therefore providing more fossil material. There are other possibilities for this apparent pattern, such as increased deposition of sediments and fossils during wetter periods, or an increase in geographic range of samples due to more active streams over a wider area. More information will be required to determine which of these possibilities is responsible for the pattern at Rodent Hill.

Table 11.1 Major sedimentary deposit type in each stratigraphic unit of Rodent Hill, compared to the total number of associated dental remains from each unit.

Strat Unit	I	II	III	IV	V	VI	VII
Sed deposit type	Fluvial	Nodular	N/A	N/A	Fluvial	Nodular	Fluvial
Total dental remains	165	28	N/A	N/A	37	3	15

12. CONCLUSIONS

The diversity of rodents at the Rodent Hill Locality is much higher than preliminary identifications demonstrated. The rodents identified from the Rodent Hill Locality are: the aplodontids *Haplomys* cf. *H. liolophus*, *Dakotallomys* cf. *D. pelycomyoides*, *Pseudallomys korthi*, *Parallomys* sp., *Campestrallomys* sp., *Prosciurus* cf. *P. parvus*, and two indeterminate species of *Prosciurus*; the sciurids *Sciurion oligocaenicus, S. xenokleitus*, *Cedromus* cf. *C. wilsoni*, *Protospermophilus,* and *Nototamias*; the heliscomyids *Heliscomys vetus, H. hatcheri,* and *H. (Syphyriomys)* sp.; the florentiamyids *Kirkomys milleri* and *Ecclesimus* sp.; the heteromyid *Proheteromys nebraskensis*; the castorids *Agnotocastor* cf. *A. praetereadens*, ?*Oligotheriomys* sp., and an indeterminate palaeocastorine; and the zapodid *Plesiosminthus* sp.

The new aplodontid species *Pseudallomys korthi* and the new sciurid species *Sciurion oligocaenicus* and *S. xenokleitus* were described. *Pseudallomys korthi* is smaller than *Pseudallomys nexodens* from the Orellan of Montana, but shares more features in common with that species than with an unnamed species of *Pseudallomys* from the Fossil Bush Locality. The *Sciurion* species are also known from the Fossil Bush Locality and the early Arikareean-age Kealey Springs Local Fauna, and may be the oldest known pteromyine squirrels.

The Rodent Hill Locality does not share a great deal of faunal similarity with any other single site. Many of the Rodent Hill taxa have been identified from South Dakota or Nebraska, but there are taxa present at Rodent Hill that are known from the Whitneyan of Montana, Wyoming and Oregon. Some taxa from Rodent Hill are only known from sites of older or younger age from North Dakota, Montana, Colorado, Wyoming and Saskatchewan.

The combination of typical Orellan and Arikareean cricetid and eomyid rodents with the Whitneyan species *Eumys brachyodus* led Rothecker (2003) to support the

Whitneyan age designation for the Rodent Hill Locality. The findings of this study further support the Whitneyan age for the Rodent Hill Locality. The Whitneyan-age rodents that have been identified from the site are *Haplomys* cf. *H. liolophus, Dakotallomys* cf. *D. pelycomyoides, Agnotocastor* cf. *A. praetereadens, Kirkomys milleri* and *Proheteromys nebraskensis*, and possibly *Cedromus* cf. *C. wilsoni*. The presence of a palaeocastorine beaver does not contradict the Whitneyan age assignment. The taxa *Prosciurus* cf. *P. parvus, Heliscomys vetus*, *H. hatcheri*, *Ecclesimus* and *Pseudallomys* are all taxa that have been described previously from Orellan sites. The genera *Parallomys, Nototamias, Protospermophilus,* and *Plesiosminthus* are previously known from Arikareean sites. The co-occurrence of these Orellan, Whitneyan and Arikareean taxa together in the same site suggests that the Rodent Hill locality should be intermediate in age, which supports the Whitneyan age assignment. Within the Cypress Hills, the Rodent Hill Locality shares taxa with both the Orellan-age Fossil Bush Locality and the early Arikareean-age Kealey Springs Local Fauna, suggesting a transition in the rodent fauna over the time represented by these sites. The combination of Orellan, Whitneyan and Arikareean (and younger) faunal elements at the Rodent Hill Locality is not considered to be the result of mixing faunas due to the co-occurrence of several taxa that were recovered *in situ* from within the stratigraphic units of Rodent Hill.

The geology of the Rodent Hill Locality is more complicated than previous surficial descriptions had indicated. The seven stratigraphic units of the site represent a cycle of fluvial deposited sands and silts; the presence of calcrete nodules indicates periods of depositional hiatus of unknown duration. More fossils are recovered from the fluvial deposit layers relative to the nodular layers.

The diversity of Whitneyan rodents is found to be much higher than previously reported (Korth, 1994a) which supports the conclusion of Rothecker (2003). In the families that were included in this study, Korth (1994a) listed 11 species. This study has described 18 species, including taxa from the families Heliscomyidae and Zapodidae, which had not been described from Whitneyan sites before. This large number of rodents from the Whitneyan supports the statement by Korth (1994a) and Rothecker

(2003) that the low number of described Whitneyan rodents was not a real phenomenon, but instead due to a lack of known microsite localities of Whitneyan age.

12.1 FUTURE WORK

Given that the Rodent Hill Locality is a Whitneyan site, study of the fauna is important for a better understanding of an age that is not well represented in the fossil record. Future studies of the other mammal groups that are present at Rodent Hill, including marsupials, “insectivores’, lagomorphs, ungulates and carnivores will definitely be necessary, and studies of the reptile and fish fossils from the site will also give insight to the faunal make-up of localities of this age.

More fossil material from the stratigraphic units of Rodent Hill will also be important in future work. The test for faunal stratification within the Rodent Hill Locality was inconclusive. More definite conclusions will require enough fossils from each stratigraphic unit to be confident that a large percentage of the fauna present has been obtained. There is still the potential that the upper part of Rodent Hill is demonstrably younger in age relative to the bottom, but no firm statement can be made at this time.

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